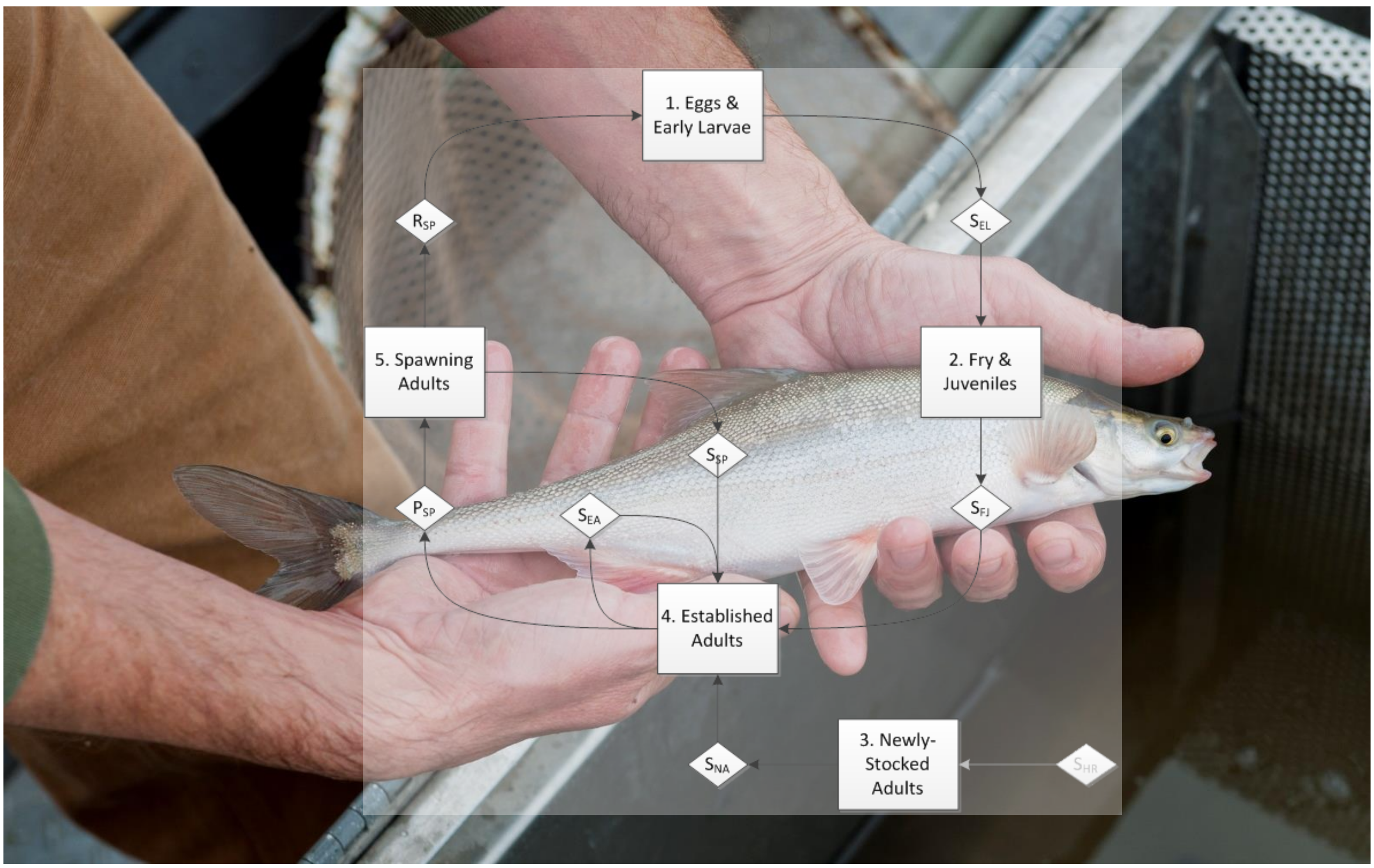
Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

Bonytail (*Gila elegans*) (BONY) Basic Conceptual Ecological Model for the Lower Colorado River



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March 2015

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Lower Colorado River Multi-Species Conservation Program

Bonytail (*Gila Elegans*) (BONY) Basic Conceptual Ecological Model for the Lower Colorado River

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ACRONYMS AND ABBREVIATIONS

BONY	bonytail (*Gila elegans*)
BP	Before Present
CEM	conceptual ecological model
cm/s	centimeters per second
DO	dissolved oxygen
g	gram(s)
kg	kilogram(s)
km	kilometer(s)
LCR	Lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
m	meter(s)
mm	millimeter(s)
mm/month	millimeter per month
NISIC	National Invasive Species Information Center
NRC	National Research Council
RASU	razorback sucker (*Xyrauchen texanus*)
Reclamation	Bureau of Reclamation
TL	total length
UCRB	Upper Colorado River Basin
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey

Symbols

≈	approximately
°C	temperature in degrees Celsius (aka Centigrade)
>	greater than
≥	greater than or equal to
<	less than
≤	less than or equal to

CONTENTS

Page

Tables

Figures

Attachments

Attachment

Foreword

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

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

- A synthesis of the current understanding of how a species' habitat works. This synthesis can be based on the published literature, technical reports, or professional experience.

- Help in understanding and diagnosing underlying issues and identifying land management opportunities.

- A basis for isolating cause and effect and simplifying complex systems. These models also document the interaction among system drivers.

- A common (shared) framework or "mental picture" from which to develop management alternatives.

- A tool for making qualitative predictions of ecosystem responses to stewardship actions.

- A way to flag potential thresholds from which system responses may accelerate or follow potentially unexpected or divergent paths.

- A means by which to outline further restoration, research, and development and to assess different restoration scenarios.

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

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

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

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

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

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

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

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

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

How to Use the Models

There are three important elements to each CEM:

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

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

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

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

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

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

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

Executive Summary

This document presents a conceptual ecological model (CEM) for bonytail (*Gila elegans*) (BONY). 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 BONY ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the methods used to measure BONY habitat and population conditions. (Note: Attachment 1 provides an introduction to the CEM process. We recommend that those unfamiliar with this process read attachment 1 before continuing with this document.)

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

CONCEPTUAL ECOLOGICAL MODELS

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

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

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

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

- **Life-stage outcomes** – These consist of the biologically crucial outcomes of each life stage, including the number of individuals recruited to the next life stage or age class within a single life stage (recruitment rate), or the number of offspring produced (fertility rate).

- **Critical biological activities and processes** – These consist of activities in which the species engages and the biological processes that take place during each life stage that significantly beneficially or detrimentally shape the life-stage outcome rates for that life stage.

- **Habitat elements** – These consist of the specific habitat conditions, the abundance, spatial and temporal distributions, and other qualities that significantly beneficially or detrimentally affect the rates of the critical biological activities and processes for each life stage.

- **Controlling factors** – These consist of environmental conditions and dynamics – including human actions – that determine the abundance, spatial and temporal distributions, and other qualities of the habitat elements for each life stage. Controlling factors are also called "drivers."

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

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

The BONY conceptual ecological model addresses the BONY population along the river and the lakes of the lower Colorado River (LCR). It does not include hatchery facilities managed exclusively for breeding BONY and rearing them to adults. However, it does include areas into which hatchery-raised BONY are released as part of the augmentation program, including ponds maintained as grow-out areas.

The basic sources of information for the BONY conceptual ecological model include the U.S. Fish and Wildlife Service (2002a); Reclamation (2005, 2008); Mueller (2006); and Pacey and Marsh (2008a). These publications summarize and cite large bodies of earlier studies; Pacey and Marsh (2008a) include summaries of additional unpublished expert knowledge specifically related to BONY rearing. 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. The purpose of this model is not to provide an updated literature review but to integrate the available information and knowledge into a CEM so it can be used to inform adaptive management.

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

1. Eggs and early larvae
    - Egg and early larval survival rate
2. Fry and juveniles
    - Fry and juvenile survival rate
3. Newly stocked adults
    - Newly stocked adult survival rate
4. Established adults
    - Established adult survival rate
    - Established adult reproductive participation rate
5. Spawning adults
    - Spawning adult fertility rate
    - Spawning adult survival rate

The model distinguishes 11 critical biological activities or processes relevant to 1 or more of these life stages, 17 habitat elements relevant to 1 or more of these critical biological activities or processes for 1 or more life stages, and

8 controlling factors that affect 1 or more of these habitat elements. Because the LCR is a highly regulated system, the controlling factors almost exclusively concern human activities.

The 11 critical biological activities and processes identified across all life stages are: chemical stress, competition, disease, drifting, egg settling and adhesion, foraging, mechanical stress, predation, resting, swimming, and thermal stress. The 17 habitat elements identified across all life stages are: aquatic macrophytes, aquatic vertebrates, birds and mammals, fishing encounters, infectious agents, invertebrates and particulate organic matter, macrohabitat geometry, mesohabitat geometry/cover, post-rearing transport and release methods, pre-release conditioning, scientific study, substrate texture/dynamics, turbidity, water chemistry, water depth, water flow/turbulence, and water temperature. The eight controlling factors identified across all habitat elements are: augmentation program operations; channel, lake, and pond design and operations; fishing activity and fisheries management; motorboat activity; nuisance species introduction and management; tributary inflows; wastewater and other contaminant inflows; and water storage-delivery system design and operations.

KEY RESULTS

The CEM identifies predation as strongly affecting all seven life-stage outcomes, but the ways in which it does so—e.g., what predators are involved, in what habitat settings—are mostly poorly understood. Foraging success directly, strongly affects four life-stage outcomes: established adult reproductive participation, established adult survival, newly stocked adult survival, and fry and juvenile survival. Foraging success also affects many life-stage outcomes indirectly through its strong effects on BONY swimming ability. As with predation, however, the effects of foraging success on life-stage outcomes—i.e., the rate at which BONY fail to forage successfully and therefore fail to survive or reproduce—are poorly understood.

The CEM identifies swimming behaviors associated with spawning as important but poorly understood factors in spawning adult survival and spawning adult fertility. Swimming abilities and behaviors also significantly affect life-stage outcomes indirectly through effects on drifting, foraging, predation, resting, and thermal stress. The understanding of these effects of swimming abilities and behaviors is mostly moderate.

Other important direct effects of critical biological activities or processes on life-stage outcomes include the effects of egg settling and adhesion on egg and early larval survival, the effects of drifting on fry and juvenile survival, and the effects of thermal stress on cues for spawning and spawning adult fertility, with varying levels of understanding. Other important indirect effects of critical biological activities and processes on life-stage outcomes include the effects of predation on egg settling and adhesion, the effects of swimming abilities on drifting behavior, and the effects of competition from other BONY and other species for habitat and food on BONY resting and foraging, with varying levels of understanding.

The CEM identifies several habitat elements that strongly and directly affect critical biological activities or processes. These pivotal habitat elements include (in alphabetical order): aquatic macrophytes, aquatic vertebrates, invertebrates and particulate organic matter, macrohabitat geometry, mesohabitat geometry/ cover, turbidity, water flow/turbulence, and water temperature. However, the vast majority of these direct effects are poorly understood.

The CEM also identifies several habitat elements that strongly but indirectly affect life-stage outcomes through the effects of these habitat elements on others with direct effects on critical biological activities or processes. The habitat elements with pivotal indirect effects include (in alphabetical order): aquatic macrophytes, aquatic vertebrates, macrohabitat geometry, mesohabitat geometry/cover, turbidity, water depth, water flow/turbulence, and water temperature. Several habitat elements thus crucially shape life-stage outcomes both through their direct effects on critical biological activities or processes and through their effects on other habitat elements.

In contrast to the direct effects of habitat elements on critical biological activities and processes, most of the indirect causal relationships among habitat elements are well understood. This understanding is based in our knowledge of hydrology, geomorphology, and limnology.

Most of the controlling factors strongly affect life-stage outcomes through their direct impacts on habitat elements. Water storage-delivery system design and operations has strong and well understood effects on macrohabitat geometry, substrate texture/dynamics, turbidity, water chemistry, water depth, water flow/turbulence, and water temperature. Channel, lake, and pond design and operations has well-understood, moderate to strong effects on macrohabitat geometry and on mesohabitat geometry/cover and medium-magnitude effects on turbidity and water depth. Tributary inflows has mostly moderately understood, moderate effects on macrohabitat geometry, mesohabitat geometry/cover, substrate texture/dynamics, water flow/turbulence, and water temperature. Nuisance species introduction and management has moderate and poorly understood effects on aquatic macrophytes, aquatic vertebrates, and invertebrates and particulate organic matter. Fishing activity and fisheries management has a strong, well understood effect on aquatic vertebrates. Wastewater and other contaminant inflows has a moderately understood, moderate effect on water chemistry. Augmentation program operations affect pre-release conditioning, with an as-yet low impact and only moderate understanding. Future efforts to pre-condition hatchery-raised BONY for release into the LCR and its isolated ponds may change this assessment.

Finally, fishing activity and fisheries management indirectly affects life-stage outcomes through its strong, well understood effect on two other controlling factors. First, fishing activity and fisheries management strongly affects nuisance species introduction and management because unregulated fishing activities have accidentally introduced, and in the future may additionally introduce, nuisance species to the LCR ecosystem. Second, fishing activity and fisheries management strongly affects augmentation program operations because the augmentation program must take into account the types and extent of fishing and fisheries management activities throughout the LCR in determining where to release hatchery-reared BONY, where fishing activities could interfere with augmentation program efforts, and how recreational fishers might help provide useful information on BONY (e.g., through creel surveys).

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

Chapter 1 – Introduction

This document presents a conceptual ecological model (CEM) for bonytail (*Gila elegans*) (BONY). 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 BONY ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the methods used to measure BONY habitat and population conditions. The CEM methodology follows that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012) with modifications. (Note: Attachment 1 provides an introduction to the CEM process. We recommend that those unfamiliar with this process read attachment 1 before continuing with this document.)

The model addresses the BONY population along the river and the lakes of the lower Colorado River [LCR] and other protected areas. The model addresses the LCR landscape as a whole rather than any single reach or managed area. It does not include hatchery and rearing facilities managed exclusively for breeding and raising BONY adults for release, but it does include protected areas into which hatchery-reared BONY are released as part of the augmentation program (Reclamation 2006).

The basic sources of the information for the BONY conceptual ecological model are U.S. Fish and Wildlife Service [USFWS] (2002a), Reclamation (2005, 2008), Mueller (2006), and Pacey and Marsh (2008a). 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. The purpose of the CEM is not to provide an updated literature review but to integrate the available information and knowledge into a CEM so it can be used to inform adaptive management.

This document is organized as follows: The remainder of chapter 1 provides an overview of the reproductive ecology of BONY as currently understood, 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 BONY in the LCR and evaluate the implications of this information for management, monitoring, and research needs.

BONY REPRODUCTIVE ECOLOGY

BONY have at least 5 million years of evolutionary history in the Lower Colorado River Basin, following earlier evolution in the Upper Colorado River Basin [UCRB] during the Miocene Epoch and the subsequent merging of the upper and lower basins (Holden and Stalnaker 1970; Douglas and Douglas 2007; Spencer et al. 2008; Ross 2013; Schönhuth et al. 2014). Consequently, BONY have a long evolutionary history of interaction with, and adaptation to, the natural environmental conditions and other endemic species of the Colorado River.

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

BONY female fecundity in the LCR generally falls in the range of 30,000–50,000 ova per kilogram (kg) of body mass (Hamman 1985; Marsh 1985). Pacey and Marsh (2008a) report body weights among the very youngest adults (approximately 150 millimeters [mm] total length [TL]) in the range of 0.05–0.25 kg, and note that older individuals in hatcheries can reach body sizes > 500 mm TL and > 1 kg. These facts together suggest overall fecundities ranging from 1,500 ova for the youngest, smallest adults up to 50,000 ova for the oldest, largest adults.

No field census data exist from which to estimate the size of the pre-regulation BONY population along the Colorado River in general, let alone just in the LCR (Minckley et al. 2003). However, based on several calculations from genetic data, Garrigan et al. (2002) (see also Minckley et al. 2003) estimate that BONY would have had to maintain a population with at least 89,500 breeding females to have maintained itself genetically in the Colorado River basin over the long term (millennia). Assuming a 1:1 adult female:male ratio, this estimate points to a minimum population size approaching 180,000 adults spanning the upper and lower basins together.

BONY unquestionably were extremely numerous in the LCR prior to the late 1800s. Prehistoric archaeological sites along the LCR valley contain large quantities of BONY bones, only exceeded (by a factor of 3) by the quantities of razorback sucker (*Xyrauchen texanus*) (RASU) bones, with the two species together comprising roughly 99 percent of all fish bones at these sites (Gobalet et al. 2005). The fish assemblages at these sites appear to have been caught in large weirs, consistent with the fishing methods of historic indigenous people in the valley (Gobalet et al. 2005). Such weirs might have been more effective at catching RASU, given the reported greater ability of BONY to escape a wide range of capture methods (Mueller 2006). The archaeological evidence therefore suggests that BONY numbers in the LCR approached those of the demonstrably formerly very abundant RASU (Minckley et al. 1991, 2003; Mueller 2006). Using the same genetic methods applied to BONY, in fact, Garrigan et al. (2002) estimated that, to have maintained itself genetically in the Colorado River over the long term (millennia), RASU would have needed a population of at least 97,500 breeding females, only slightly higher than the estimate for BONY.

BONY can live for 30 years or longer (Garrigan et al. 2002; Minckley et al. 2003; Mueller 2006) and, under natural conditions, could spawn multiple times over their lifetimes (see chapters 2, 3, and 6). A hypothetical female that spawned only five times over a 30-year lifespan under natural conditions thus might produce roughly 129,000 ova over that lifespan, and only 2 of these ova would need to grow into sexually mature offspring for the parents to replace themselves in the population. BONY thus had a very low natural average lifetime reproductive success rate of perhaps only 0.00155 percent (roughly 1.5 out of every 100,000 ova). Studies are underway to provide a more accurate estimate of the fraction of BONY that may participate in spawning per year (see chapter 2).

The timing of BONY spawning in the LCR correlates seasonally with the rise in water temperature following the winter low (see chapters 2–4). This timing usually precedes the Colorado River spring flood pulse that normally occurs following snowmelt in the Rocky Mountains (Mueller 2006). BONY deposit their eggs into the substrate, where they must remain to develop and hatch. Spawning sites therefore must provide substrates that remain stable over the course of embryo development, hatching, and larval development prior to swim-up. Otherwise, eggs and small larvae in/on these substrates could be churned up, buried, or exposed during the rise and fall of the spring flood pulse. The timespan in the wild during which BONY embryo and early larvae (prior to swim-up) are vulnerable to disruption of their natal site ranges from 6 to 11 days at 18–20 degrees Celsius (°C) (see chapter 2). Further, BONY spawn in locations at some distance from locations suitable for nursery habitat. BONY larvae therefore must find their way to suitable nursery habitat following swim-up (see chapters 3, 4, and 6). However, BONY immediately following swim-up (approximately 15–25 mm TL) lack the strength or environmental familiarity to navigate in the river and depend on currents (drifting) to transport them into nursery habitat. Excessively weak or strong currents from a drought or flood pulse during this period of drift could transport the tiny larvae too little or too far, preventing their settling into suitable nursery habitat. Flood pulse variability therefore would have posed significant risks for BONY larval survival.

Once they reach suitable nursery habitat, young BONY in the wild mature to adulthood in approximately 4–6 months (see chapter 2) (Mueller 2006, 2007; Pacey and Marsh 2008a; Sykes 2013). Suitable natural nursery environments appear to include shallows, connected backwaters, and lakes and wetlands formed by flood-pulse inundation of the flood plain (see chapters 3, 4, and 6). These environments had to remain connected to the river, or become reconnected before drying out following spring flooding, to allow the maturing BONY to move into the larger ecosystem as they approached or reached adulthood. Flood plain ponds that became disconnected from the river would have become inhospitable to juvenile BONY due to rising water temperatures and salinity as they dried out. BONY fry and juveniles in wild nursery habitats therefore faced yet additional environmental risks for surviving to adulthood.

Historically, the timing and magnitude of the Colorado River spring flood pulse in fact varied greatly from year to year and over longer timespans (Ely et al. 1993; O'Connor et al. 1994; Woodhouse et al. 2010; Reclamation 2011a). In turn, Piechota et al. (2004) identified approximately 11 droughts lasting 5 years or more, affecting the discharge of the Colorado River between 1923 and 2004. In turn, Woodhouse et al. (2010) identified numerous short- and long-term droughts over the preceding 1,200 years, providing a larger context for understanding the historic record. A severe drought in 2000–2004, for example, produced the lowest 5-year period of flow on the Colorado River in the historic gauge record up to that time (1906–2005) but ranked as only the seventh worst drought in the last 500 years (Piechota et al. 2004; Woodhouse et al. 2010). The timing of the annual flood pulse in the LCR varies with the timing of the onset of snowmelt in different parts of the Rocky Mountains and the timing of spring rain storms, including rain-on-snow events. Prolonged droughts can put aquatic species under severe selective pressure, force them into refugia, and create genetic bottlenecks. For example, 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 intermountain western North America ca. 7500 years BP. Douglas et al. (2003) did not assess evidence for a similar bottleneck for BONY, but the same drought would have affected all large-river fish species along the river (see also Douglas and Douglas 2007; Hopken et al. 2012). Over the centuries, therefore, the spring period of BONY spawning, larval dispersal, and maturation in nursery habitat has always been a period of wide hydrologic variability.

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

Over the centuries, therefore, the spring period of BONY spawning, larval dispersal, and maturation in nursery habitat was always a period of wide temperature variability in the LCR, independent of the variability in riverflows.

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

The evidence therefore suggests that environmental variability naturally would have subjected BONY to significant mortality during the first few weeks and months following spawning. This high rate of mortality would have been compounded by a high rate of predation as well. Many native aquatic species would have consumed BONY eggs, including adult BONY and RASU (Mueller 2006) (see chapter 6). The concentration of eggs at spawning sites makes them particularly vulnerable to consumption; their availability during the late winter or early spring would provide a food resource during a season of otherwise low productivity (Mueller 2006). Additionally, numerous native species also likely prey on BONY larvae, fry, and juveniles, including the carnivorous larvae of several native insects (Horn et al. 1994; Mueller 2006) (see chapters 3, 4, and 6). BONY egg, larval, fry, and juvenile 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 BONY reproductive strategy therefore may be adapted to the extremely low probabilities of survival faced by individual embryos (Mueller 2006). The vast majority of eggs, larvae, and fry would die in most years, but enough would survive in enough years to perpetuate the species. Juvenile and adult survival may not have been easy either, but it would have been less tenuous. For example, juvenile and adult BONY in natural settings would naturally have faced competition for food from other BONY and other native species as well as predation from native species such as the Colorado pikeminnow (*Ptychocheilus lucius*) (see chapters 2, 4, and 6). However, BONY naturally grow rapidly over their first two to three years (see chapter 2) and develop a characteristic modest bony nuchal hump. These changes would have reduced the diversity of both the competition and predation they faced as they matured (see chapter 6). In addition, BONY become sexually mature within their second year of life (see chapter 2), ready to start trying to produce offspring of their own.

CONCEPTUAL ECOLOGICAL MODEL PURPOSES

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

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

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

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

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

The CEM methodology used here expands on that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012). The expansion incorporates recommendations of Wildhaber et al. (2007, 2011), Kondolf et al. (2008), and Burke et al. (2009) to provide greater detail on causal linkages and outcomes, and explicit demographic notation in the characterization of life-stage outcomes (McDonald and Caswell 1993). Attachment 1 provides a detailed description of the methodology. The resulting 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 reproduction, and the biologically crucial outcomes of each life stage. These biologically crucial outcomes typically include the number of individuals recruited to the next life stage (e.g., juvenile to adult) or next age class within a single life stage (recruitment rate), and the number of viable offspring produced (fertility rate). The CEM then identifies the factors that shape the rates of these outcomes in the study area and thereby shapes the abundance, distribution, and persistence of the species in that area.

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

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

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

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

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

- **Controlling factors** – These consist of environmental conditions and dynamics—including human actions—that determine the quality, abundance, and spatial and temporal distributions of important habitat elements. Controlling factors are also called "drivers." 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 spawning sites may depend on factors such as river flow rates, sediment transport rates, and flow-path morphology. The status of these factors, in turn, may depend on factors such as dam design, reservoir morphology, and dam operations, which, in turn, are shaped by watershed geology, vegetation, climate, land use, and water demand.

The CEM identifies these five components and the causal relationships among them that affect life-stage outcome rates. 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 rates of its life-stage outcomes, support or limit the rate of each critical biological activity or process, and support or limit the quality, abundance, and distribution of each habitat element (as these affect other habitat elements or affect critical biological activities or processes). In addition, the 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 1 provides further details on the assessment of causal relationships, including the use of diagrams and a spreadsheet tool to record the details of the CEM and summarize the findings.

Chapter 2 – BONY Life Stage Model

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

The literature on BONY in the Upper and Lower Colorado River Basins does not follow any single classification of BONY life stages. In fact, few publications provide or summarize information on all stages of BONY life history. The species almost disappeared in the wild before intensive study of its life history could begin (USFWS 1990; Minckley 1991). Since that time, researchers have struggled to fill in crucial gaps in knowledge based on scattered observations of the species in open waters along with more frequent observations in protected ponds, hatcheries, and rearing facilities. USFWS (2002a), Mueller (2006), Pacey and Marsh (2008a), and Reclamation (2008) provided extensive overlapping bibliographies. Valdez et al. (2011) presented a conceptual life history model for BONY in the UCRB, including an explicit designation of life stages and lists of biotic and abiotic controlling factors but also noted how little information is available to support their designations.

EVIDENCE FOR BONY LIFE STAGES

USFWS (2002a), Mueller (2006), Pacey and Marsh (2008a), and Reclamation (2008) summarized evidence indicating that BONY spawn as early as their second year (Age-1), after achieving a body size of approximately (≈) 100 mm TL, but more commonly first spawn in their third year (Age-2). Females > 100 mm TL can express eggs and can carry eggs massing up to 20–30 percent of their total body weight. The number of eggs produced per female in the LCR, estimated from egg mass, increases with body mass (Hamman 1982, 1985). As noted in chapter 1, BONY female fecundity in the LCR is approximately 30,000–50,000 ova per kilogram of body mass (Hamman 1985; Marsh 1985). Marsh (1985) reported a fecundity of 30,000 ova from a female 490 mm TL weighing 1,000 grams (g); Pacey and Marsh (2008a) reported older individuals in hatcheries can reach body sizes of > 500 mm TL and > 500 g.

BONY appear to be skip spawners (Johnston 1999), a species in which only a portion of the adult population breeds in any given year. Adult BONY develop secondary sexual traits in both sexes over the course of several months prior to their participation in spawning (Hamman 1982, 1985; USFWS 2002a; Mueller 2006; Pacey and Marsh 2008a). Development of secondary sexual traits and production of gametes presumably require a suitable level of fitness since they divert energy from other physiological processes. Development of secondary sexual traits and production of gametes presumably are triggered at least in part by cues in the water, the identities and mechanisms of which are not currently known. Data are not yet available on the annual rate of reproductive participation – the percentage of adults that participate in and contribute gametes to spawning per year. However, studies are underway that could provide estimates under LCR MSCP Work Task C40, Genetic and Demographic Studies to Guide Conservation Management of Razorback Sucker and Bonytail in Off-Channel Habitats (Reclamation 2014).

BONY spawning presumably is triggered by environmental conditions, with a change in water temperature the most likely or dominant trigger. Specifically, spawning takes place preferentially when the water temperature rises to ≈ 18 °C at the beginning of the spring season. Consequently, as noted by Minckley (1991) and Mueller (2006), spawning occurs earlier to the south and later to the north, coinciding roughly with the arrival of water temperatures in the range of 18–20 °C. Spawning occurred in early March–April at Cibola High Levee Pond in 2000–2005, although it historically may have occurred even earlier in the Colorado River Delta. In Lake Mohave, LCR, spawning historically occurred in May and as late as early July in the Green River, UCRB. The cited temperature range for spawning also appears to be optimal for hatching the greatest numbers of viable larvae (Hamman 1982, 1985; Marsh 1985; Mueller 2006; Kappenman et al. 2012). Whether other triggers, such as changes in riverflow or pheromones, are involved is currently not known. For example, Mueller (2006) noted that the timing of spawning coincides with the normal rising limb of the spring high-flow pulse along the LCR. However, BONY spawn in isolated ponds along the LCR with non-riverine hydrologic regimes. This latter fact suggests that BONY can spawn without any cues from the flow regime at all (Mueller 2006; Kesner et al. 2010a, 2010b; LCR MSCP biologists 2013, personal communications).

Spawning BONY aggregate in large numbers at individual spawning sites: Jonez and Sumner (1954) described an aggregation of approximately 500 individuals at a single spawning event in the nascent Lake Mohave, and Mueller (2006) described spawning at Cibola High Levee Pond as occurring in “tight schools.”

Spawning can occur on both natural and artificial substrates, including at hatcheries (Pacey and Marsh 2008a), sometimes interfering with hatchery efforts to control breeding (Mueller 2006; Kesner et al. 2010a, 2010b). USFWS (2002a), Mueller (2006), and Reclamation (2008) summarized evidence that BONY spawning outside hatcheries takes place in distinct settings visited specifically for spawning. Spawning takes place at sites other than where BONY live during the rest of the year; BONY consequently must move across some distance to reach a spawning site. However, Mueller (2006) noted that BONY move no more than 10 kilometers (km) per day to reach spawning sites and may travel only minutes or, at most, a very few days to reach a spawning site. Common features of all spawning sites include a relatively uniform range of substrate particle sizes free of silt and other fine sediment and a location adjacent to deeper water (Mueller 2006; Kesner et al. 2010a, 2010b). BONY spawning sites outside of hatcheries may lie immediately adjacent to normal feeding and resting habitat, as investigators observed in Cibola High Levee Pond in Cibola National Wildlife Refuge (Mueller 2006), and as suspected to have occurred in Imperial Pond 2 (Kesner et al. 2010b). BONY preferences for spawning habitat and spawning site fidelity are topics of ongoing investigations funded under the LCR MSCP. Specifically, studies are ongoing under LCR MSCP Work Tasks C25, Imperial Ponds Native Fish Research; C40, Genetic and Demographic Studies to Guide Conservation Management of Razorback Sucker and Bonytail in Off-Channel Habitats; and C41, Role of Artificial Habitat in Survival of Razorback Sucker and Bonytail (Reclamation 2014).

Only a few investigators have observed BONY spawning in natural settings (Vanicek and Kramer 1969; Minckley 1991; Mueller 2006). The few observations reported indicate that spawning takes place over a span of seconds to minutes in waters 0.5–10 meters (m) deep (Mueller 2006). Three to five males spawn with each female (Mueller 2006), but field records do not indicate whether individual males spawn with more than one female over the course of an overall spawning event. Jonez and Sumner (1954) reported that gill netting over the BONY spawning event they observed in the nascent Lake Mohave resulted in 42 males and 21 females being caught, suggesting that males may greatly outnumber females at individual spawning sites. Mueller (2006) cited data that BONY spawning can take place during the day and at night, and that younger/smaller individuals at Cibola High Levee Pond (at Cibola National Wildlife Refuge), 2000–2005, tended to spawn during the day and older/larger individuals at night. BONY females broadcast their eggs over the substrate (Jonez and Sumner 1954; Mueller 2006), and both males and females “fin” over the area of release from close to the substrate surface, driving the eggs into the substrate (Mueller 2006). Other BONY, reportedly not the spawners (Mueller 2006), charge into the broadcast areas and push their snouts into the substrate to locate and consume the eggs. Non-native carp also may forage for freshly deposited BONY eggs (Bozek et al. 1984). In turn, this combination of finning and attacks by would-be predators may churn the substrate, hiding at least some of the eggs from consumption (Mueller 2006).

BONY eggs that remain on or in the substrate following spawning adhere to and mature in the substrate and harden within 1–2 hours (Marsh 1985; Mueller 2006), with no parental investment. They are vulnerable to predation (see above), to fungal and presumably other types of infection, and potentially to degraded water quality during this time (Bulkley et al. 1982; Hamman 1982, 1985; Marsh 1985; USFWS 2002a; Mueller 2006; Pacey and Marsh 2008a; Reclamation 2008). The rate of embryo maturation is temperature sensitive, with the optimal temperature for hatching the greatest proportion of viable larvae in the range of 18–21 °C (Bulkley et al. 1982; Hamman 1982, 1985; Marsh 1985; Mueller 2006; Pacey and Marsh 2008a; Kappenman et al. 2012).

Larvae are 6.0–6.3 mm TL upon hatching, after ≈ 100–160 hours at 20 °C following fertilization (Hamman 1982; Marsh 1985). Some investigators refer to newly hatched BONY larvae as "fry," but distinguish them from "swim-up fry." Valdez et al. (2011) also suggested distinguishing larvae before versus after swim-up for purposes of life history classification. Marsh (1985) reported that BONY larvae at swim-up are larger (8.6 mm) at 20 °C versus 15 or 26 °C. Marsh (1985) also reported that larvae require approximately 80–90 hours at 20°C to reach swim-up following hatching, whereas Hamman (1982) reported a value of only 48 hours for this interval at the same temperature.

Mueller (2006) used the term "fry" to refer to larvae following swim-up and described "fry and juveniles" as having lengths of 15–100 mm TL. Pacey and Marsh (2008a) classified individuals ≤ 25 mm TL as "larvae" and 26–150 mm TL as "juveniles." They also noted that larvae and early juveniles grow rapidly, 17–38 RR85827000) TL, but mostly in the range of 25–30 mm/month TL, in both natural and artificial settings.

The habitat conditions that BONY seek for spawning do not appear to coincide with the conditions needed for larval nursery habitat (Mueller 2006). Following swim-up, therefore, BONY larvae must find and settle in suitable nursery habitat despite their limited swimming abilities. BONY spawning and post-spawning behaviors evolved in riverine settings, where its larvae could reach suitable nursery habitat primarily only through drift. Drawing an analogy with RASU, Valdez et al. (2011) proposed distinguishing a life stage for BONY spanning the period of dispersal of larvae from spawning sites to nursery habitat. Unique features of this proposed life stage include the importance of drift in the dispersal process and the exposure of the larvae to ready predation along their drift path. Valdez et al. (2011) also proposed distinguishing a second larval life stage spanning the period of development of larvae into juveniles in nursery habitats.

However, it may not be useful for the present BONY conceptual ecological model to distinguish between dispersing larvae and larvae settled in nursery habitat. For example, no evidence exists indicating whether BONY larvae in natural settings remain at just one nursery site following their initial dispersal or move among several sites as they mature. Further, little is known about the locations of BONY spawning and nursery sites prior to river regulation. As a result, the available information does not indicate how proximate suitable nursery habitat may have been to spawning areas prior to regulation and therefore how far BONY larvae would have drifted following swim-up.

Several experts have suggested that predation on dispersing larvae would favor the survival of those larvae with the shortest dispersal routes, particularly routes with good cover (e.g., Mueller 2006; Kesner et al. 2010a, 2010b). These suggestions rest on observations of isolated ponds in which BONY have voluntarily spawned and subsequently persisted, where suspected nursery habitat lay close to known or suspected spawning areas with little or no intervening "dispersal" habitat (Mueller 2006; Kesner et al. 2010a, 2010b).

The onset of sexual maturation may occur as early as 64 days following hatching, which should correspond to a size range of 60–70 mm TL. Mueller (2007) cited 100 mm TL for earliest onset and reported that females subsequently may grow faster than males. Pacey and Marsh (2008a) reported a wide range of variation in how quickly maturation occurs in relation to water temperatures and food availability. Mueller (2006) classified individuals > 100 mm TL as adults, while Pacey and Marsh (2008a) set the threshold slightly higher, at > 150 mm TL. Given the growth rates observed among larvae and juveniles (see above), BONY thus become adults within 4–6 months after hatching, Age-0. Evidence summarized by Pacey and Marsh (2008a) from both natural and artificial settings indicate that the rate of growth subsequently declines, to an average of roughly 10–13 mm/month TL during the second year (Age-1), 5–7 mm/month TL in the third year (Age-2), and 4 mm/month TL thereafter. Adults historically achieved lengths > 500 mm TL but usually less; today, individuals > 400 mm are rare, and most achieve lengths in the range of 300–400 mm TL (Minckley 1991; USFWS 2002a; Mueller 2006; Pacey and Marsh 2008a; Reclamation 2008).

Stocking from hatchery broodstock is the overwhelming source of adults in open environments along the LCR today; contributions from wild-reproducing BONY are thought to be minimal. A goal under the augmentation program is to release BONY from hatcheries when they reach ≈ 300 mm TL (305 mm TL in California). Sykes (2011) reported that BONY in hatcheries require 8 months to 2 years to achieve lengths > 300 mm TL (varying in part with fish density). However, BONY in hatcheries can vary greatly in size within a single cohort. As a result, hatcheries cannot easily separate BONY by size when preparing a cohort for release, and releases may include individuals as small as 250 mm TL (Pacey and Marsh 2008a; LCR MSCP biologists 2014, personal communications).

Fry/juveniles and adults exhibit ranges of defensive and avoidance behaviors in response to predator activity, including hiding in geomorphic and vegetative cover (Mueller 2006; Marsh et al. 2013b). Cover types used include dark interstices among cobbles and boulders; entrances to beaver dams; bedrock crevices and overhangs; dense submerged, emergent, and overhanging vegetation; and floating vegetation mats. Defensive behaviors include schooling and "scrumming" (Mueller 2006). It is not clear whether or how such behaviors differ between juveniles and adults. Adults may be territorial or have strong fidelity to a particular "home" habitat area.

PROPOSED BONY LIFE STAGES

The evidence summarized above suggests that the CEM for BONY should recognize five life stages and seven life-stage outcomes as follows and as illustrated on figure 1.

1. **Eggs and early larvae:** This life stage begins with the end of involvement of the spawning adults in the fate of the eggs, probably after finning, when the spawning individuals depart the scene of each individual spawning event, continues through egg incubation and hatching, and ends with larval swim-up, which presumably occurs at approximately 15 mm TL. The life stage has a single life-stage outcome, designated in figure 1 as S_{EL}, the rate of survival of (recruitment from) the life stage.

2. **Fry and juveniles:** This life stage covers the time from larval swim-up and dispersal to sexual maturation, beginning at roughly 15 mm TL and extending to roughly 100–150 mm TL. There is currently insufficient information to justify subdividing this overall developmental span (e.g., by distinguishing the period of larval dispersal from the period of maturation in nursery habitat as separate life stages). The present BONY conceptual ecological model therefore takes the simpler approach of treating fry (larvae following swim-up) and juveniles together in a single life stage, pending improved knowledge of this portion of the BONY life cycle. The life stage has a single life-stage outcome, designated S_{FJ}, the rate of survival of (recruitment from) the life stage.

3. **Newly stocked adults:** This life stage covers adults newly released from hatcheries, during their initial acclimation to river, reservoir, or grow-out pond conditions. Hatchery breeding is the overwhelming source of BONY in the LCR and its reservoirs. Newly stocked adults may remain behaviorally distinct from wild-born (but currently rare) BONY for some time after release. The component has a separate input, S_{HR}, for the rate of stocking from hatcheries, but this input and the hatchery programs behind it are not part of the CEM. The life stage has a single life-stage outcome, designated S_{NA}, the rate of survival of the newly stocked adults to become established adults.

4. **Established adults:** This life stage covers the entire lifespan for adults established in open habitats, including grow-out ponds but not hatcheries. The life stage has two life-stage outcomes: (a) S_{EA}, the rate of survival of established adults from year to year so that they remain part of the adult population, and (b) P_{SP}, the rate of reproductive participation – the percentage of adults that participate in and contribute gametes to spawning per year.

5. **Spawning adults:** This life stage covers adults that move to spawning sites to participate in spawning. The component begins when would-be spawners leave their normal territories to move toward spawning sites and ends when these individuals return to their normal territories. The life stage has two life-stage outcomes: (a) S_{SP}, the rate of survival of spawning adults to return to the adult population following spawning, and (b) R_{SP}, the rate of production of fertilized eggs (fertility rate) at spawning sites.

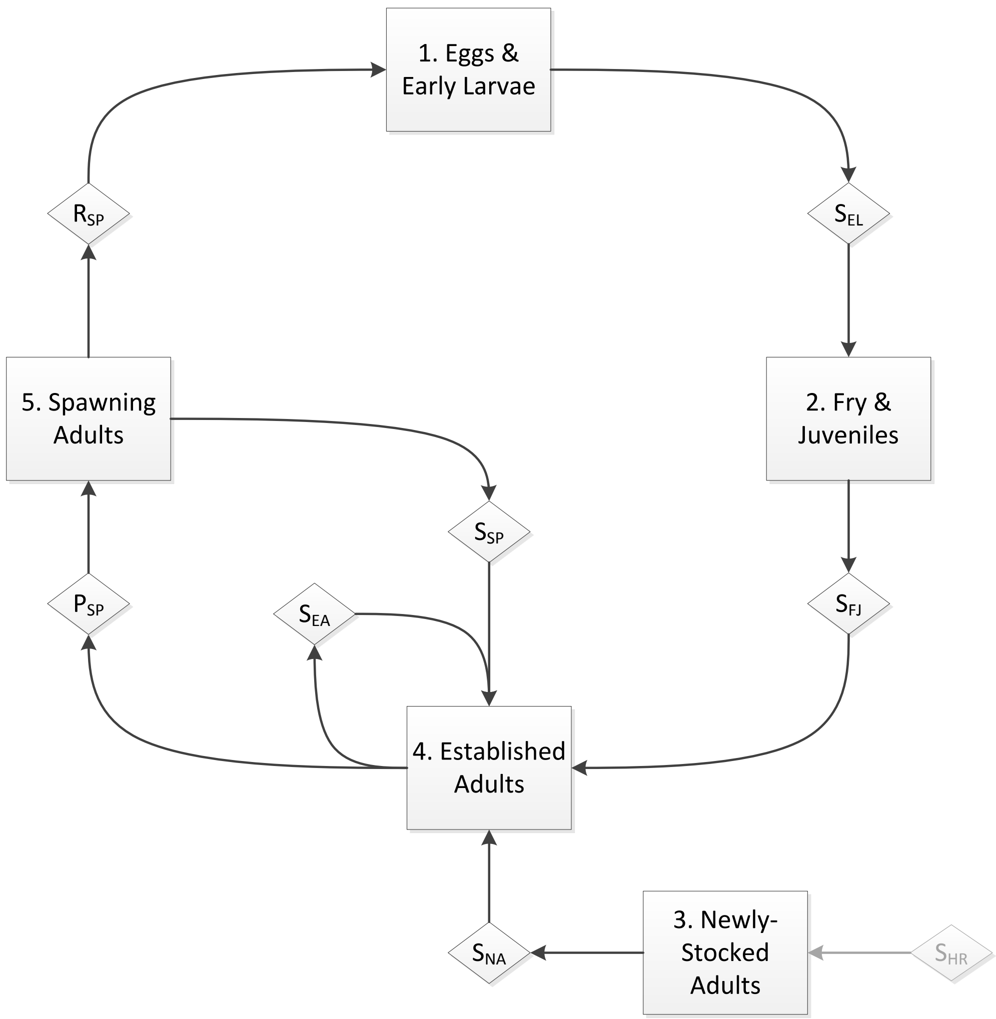


Figure 1.—Proposed BONY life history model.
Squares indicate the life stage, and diamonds indicate life-stage outcomes. S_{EL} = the rate of survival of (recruitment from) the life stage, S_{FJ} = the rate of survival of the life stage, S_{HR} = rate of stocking from hatcheries (this input and the hatchery programs behind it are not part of the CEM), S_{NA} = the rate of survival of the newly stocked adults to become established adults, S_{SP} = the rate of survival of spawning adults to return to the adult population following spawning, S_{EA} = the rate of survival of established adults from year to year so that they remain part of the adult population, P_{SP} = the rate of reproductive participation, i.e., the percentage of adults that participate in and contribute gametes to spawning per year, and R_{SP} = the rate of production of fertilized eggs per spawning adult at spawning sites.

Table 1 and figure 1 summarize this proposed model of BONY life stages and life-stage outcomes. Figure 1 also indicates the importance of the hatchery breeding program as the major source of adults in the river, reservoirs, and ponds. However, the present CEM does not address the internal workings of the hatchery breeding program. The life stages are numbered sequentially beginning with the eggs and early larvae.

Table 1.—BONY life stages in the LCR ecosystem

Life stage	Life-stage outcome(s)
1. Eggs and early larvae	• Egg and early larval survival rate
2. Fry and juveniles	• Fry and juvenile survival rate
3. Newly stocked adults	• Newly stocked adult survival rate
4. Established adults	• Established adult survival rate • Established adult reproductive participation rate
5. Spawning adults	• Spawning adult fertility rate • Spawning adult survival rate

These life stages provide the foundation for a CEM addressing BONY demography and distribution in the LCR. However, a CEM for BONY also needs to address species genetic integrity. The BONY augmentation program relies on a small and genetically constricted broodstock (Hampton 2011). In addition, BONY are members of the "*Gila* complex" (aka the "*Gila robusta* complex") of closely related species, genus *Gila*, endemic to the Colorado River basin. In addition to BONY, the complex includes humpback chub (*G. cypha*), roundtail chub (*G. robusta*), and several subspecies of *G. robusta*. Numerous investigators have identified hybrids among all three full species (*G. cypha*, *elegans*, and *robusta*) in open waters and observed mixed-species spawning at hatcheries (Minckley 1991; Gerber et al. 2001; USFWS 2002a; Douglas and Douglas 2007). Investigators have proposed that hybridization occurred naturally within the *Gila* complex prior to river regulation, and/or that river regulation has promoted hybridization by confining population fragments of *G. cypha*, *elegans*, and *robusta* together in small refugia, in which their spawning areas may overlap (Gerber et al. 2001; USFWS 2002a; Douglas and Douglas 2007).

The USFWS amended recovery goals for BONY (USFWS 2002a) includes goals for both demographic and genetic viability. Managers of the hatchery broodstock bear the responsibility for sustaining and enhancing the genetic viability of the broodstock, which the CEM does not address. However, species managers also may need to know how various causal factors affect the genetic diversity of the eggs fertilized at "wild" spawning sites (see above, "5. Spawning Adults," outcome R_{SP}, the rate of production of fertilized eggs at spawning sites). The CEM addresses the genetic integrity of non-hatchery spawning output across the LCR and its protected areas by stipulating that outcome R_{SP} in the model refers exclusively to **non-hybrid** fertilized eggs.

Chapter 3 – Critical Biological Activities and Processes

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

The CEM identifies 11 critical biological activities and processes that affect one or more BONY life stages. Some of these biological activities or processes differ in their details among life stages. For example, BONY of different life stages differ in their swimming agility, strength, and stamina. However, grouping activities or processes into broad types across all life stages makes it easier to compare the individual life stages to each other across the entire life cycle. Table 2 lists the 11 critical biological activities and processes and their distributions across life stages.

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

Life stage ➔ **➔ Critical biological activity or process**	Eggs and early larvae	Fry and juveniles	Newly stocked adults	Established adults	Spawning adults
Chemical stress	X	X	X	X	X
Competition		X	X	X	
Disease	X	X	X	X	X
Drifting		X			
Egg settling and adhesion	X				
Foraging		X	X	X	
Mechanical stress	X	X	X	X	X
Predation	X	X	X	X	X
Resting		X	X	X	
Swimming		X	X	X	X
Thermal stress	X	X	X	X	X

The basic sources of the information used to identify BONY critical biological activities and processes across all life stages are USFWS (1990, 2002a), Minckley (1991), Reclamation (2004, 2008), Mueller (2006), Pacey and Marsh (2008a), and Valdez et al. (2011). The identification 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 11 critical biological activities and processes in alphabetical order.

CHEMICAL STRESS

BONY in every life stage, as with all freshwater fishes, are vulnerable to stress and mortality due to an insufficient supply of dissolved oxygen (DO), insufficient removal of wastes, exposure to unsuitable levels of salinity, and exposure to harmful dissolved contaminants (Bulkley et al. 1982; Buhl and Hamilton 1996; Buhl 1997; Canton 1999; Tomasso et al. 2003; Dwyer et al. 2005; Pacey and Marsh 2008a; Walker et al. 2009). 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 BONY mature, they presumably become increasingly able to avoid or remove themselves from settings in which they sense chemically unsuitable conditions—if these conditions are sufficiently localized to permit such avoidance or escape.

COMPETITION

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

DISEASE

BONY in every life stage are vulnerable to infection, including by fungi and parasites (Flagg 1982; Hamman 1982; Bozek et al. 1984; Marsh 1985; Tyus et al. 1999; Hansen et al. 2006, 2007; Mueller 2006; Bestgen et al. 2008; Pacey and Marsh 2008a; Portz 2009; Archdeacon et al. 2010; Sykes 2011; Linder et al. 2012; Marsh et al. 2013a). Non-lethal infections may make the affected individuals vulnerable to mortality from other causes.

DRIFTING

BONY fry and juveniles in riverine settings presumably drift in currents to move from their natal sites to their nursery sites or among nursery sites, although hatcheries and isolated ponds may provide little opportunity for such behavior (Mueller 2006). Lateral and reverse currents in natural river channels, such as those in eddies, transport drifting fry into and out of high- versus low-velocity settings along their drift paths. Channel sections along which lateral and reverse currents draw drifting fry out of the main line of downstream flow into low-velocity settings such as shoreline embayments may be termed “interception habitats.” (The term originates in a CEM developed for the endangered pallid sturgeon [*Scaphirhynchus albus*] to support species recovery along the Missouri River [W. Nelson-Stastny 2015, personal communication]). BONY fry and juveniles also may control the timing of their drift by swimming in/out of currents, as do other fishes in the LCR (Modde and Haines 2005; Valdez et al. 2011). They also may preferentially drift at night (Snyder and Meisner 1997), a behavior that may reduce predation, as has been proposed for other LCR fishes (Johnson et al. 1993; Horn et al. 1994; Johnson and Hines 1999).

EGG SETTLING AND ADHESION

Spawning BONY broadcast their eggs and sperm together over the substrate, and fertilization takes place on or above the substrate surface (Marsh 1985; Hamman 1982, 1985; Minckley 1991; USFWS 2002a; Reclamation 2005, 2008; Mueller 2006; Pacey and Marsh 2008a; Valdez et al. 2011). After fertilization, the eggs must settle into the substrate, harden, and adhere to the substrate. Males and females may “fin” over the area of release, from close to the substrate surface, driving the fertilized eggs into the substrate (Mueller 2006). Other BONY, reportedly not the spawners (Mueller 2006), charge into the broadcast areas and push their snouts into the substrate to locate and consume the eggs. However, this activity also churns the substrate, hiding at least some of the adhered eggs from consumption (Mueller 2006).

FORAGING

Newly hatched BONY begin foraging once they have assimilated their yolk and become able to swim, and they continue foraging through all remaining life stages. Outside of hatcheries, BONY are omnivorous. Analyses of stomach contents and field observations indicate that BONY feed on plant litter; aquatic macrophytes; phytoplankton and zooplankton; macroinvertebrates, such as aquatic insect adults and larvae, and crayfish; terrestrial insects that may fall or land on the water; and small vertebrates such as bullfrog larvae and small fish (Vanicek and Kramer 1969; Tyus and Minckley 1988; Lenon et al. 2002; USFWS 2002a; Marsh and Schooley 2004; Mueller 2006; Reclamation 2008; Marsh et al. 2013a). The proportion of larger prey in their diet increases and the proportion of plant matter decreases as BONY increase in size (Mueller 2006). Field observations indicate that they feed mostly at night (Mueller 2006; Marsh et al. 2013b, 2013a), may feed on RASU eggs and their own eggs (Mueller 2006), and feed on different foods in different environments, indicating wide dietary flexibility (USFWS 2002a; Marsh and Schooley 2004). BONY adult morphology, specifically its subterminal mouth position, suggests adaptation to both benthic and open-water feeding (Mueller 2006).

MECHANICAL STRESS

BONY in every life stage are vulnerable to stress and outright physical destruction due to mechanical impacts, abrasions, burial, or exposure. BONY in the LCR may encounter many situations that result in mechanical stress, including encounters with propeller blades, propeller wash, or a jet-ski intake; entrainment by flow velocities and turbulence in excess of tolerable ranges, such as near irrigation diversions; burial by a rapid influx of sediment; stranding by a sudden drop in water level; inundation by water levels too deep for embryos to mature; recreational fishing catch and release; unsuccessful predator attacks; scientific sampling; and transport and release from rearing facilities (Bozek et al. 1984; USFWS 2002a; Mueller et al. 2005; Paukert et al. 2005; Mueller 2006; Bestgen et al. 2008; Pacey and Marsh 2008b; Ward et al. 2008; Portz 2009; Sykes 2011, 2013; Hunt et al. 2012). Mechanical stress that does not result in BONY mortality nevertheless may leave the affected individuals more vulnerable to infections and mortality from other causes (Mueller 2006; Mueller et al. 2007). As BONY mature, their increasing strength should make it possible for them 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.

PREDATION

BONY experience mortality due to predation during every life stage, as do all wild animals. Every animal species has evolved 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 losses from predation.

BONY face predation from both aquatic and avian species, and possibly also from terrestrial mammals such as raccoons and ringtail cats that may hunt along shorelines (Mueller 2006). As discussed further in chapters 4 and 6, BONY in each life stage may experience predation from a distinct spectrum of these species (and sometimes different life stages among these species) with differing predatory behaviors (Bozek et al. 1984; USFWS 1990, 2002a; Minckley 1991; Lentsch et al. 1995; Minckley et al. 2003; Mueller 2005; Christopherson et al. 2004; Brunson and Christopherson 2005; Marsh and Pacey 2005; Modde and Haines 2005; Mueller 2005, 2006, 2007; Mueller et al. 2006, 2007; Reclamation 2006, 2008; Bestgen et al. 2008; Kesner et al. 2008, 2010a, 2010b; Pacey and Marsh 2008b; Karam and Marsh 2010; Karam et al. 2013; Ward and Figiel 2013).

The historic, unregulated river supported far fewer predatory species than does the present-day system but nevertheless would have shaped the evolution of both behavioral and morphological adaptations in BONY to predation. The Colorado pikeminnow was the only large predatory fish in the LCR (Minckley 1973; USFWS 2002b; Portz and Tyus 2004; Franssen et al. 2007; D. Ryden 2013, personal communication; San Juan River Basin Recovery Implementation Program Web site, http://www.fws.gov/southwest/SJRIP/GB_FS.cfm). The species lacks teeth in its jaws and instead uses pharyngeal teeth to grasp and hold its prey. Pikeminnow adults often exceed 500 mm TL and have been recorded to approach 1800 mm TL (USFWS 2002b). They become exclusively piscivorous after reaching ≈ 200 mm TL. Their selection of prey is strongly gape limited (Vanicek and Kramer 1969; Portz and Tyus 2004).

Franssen et al. (2007) and Ryden (2013, personal communication) estimated that pikeminnow prefer deep-bodied prey no more than 33–37 percent of their own body length. Based on size preferences, a 500-mm TL pikeminnow thus would prey on fishes less than 165–185 mm TL, and a 1,000 mm TL pikeminnow would prey on fishes less than 330–370 mm TL. These measurements place BONY of all ages (Vanicek and Kramer 1969) within the size range of pikeminnow prey. Further, pikeminnow consume primarily small-bodied, soft-rayed, cylindrical prey lacking a dorsal keel (Vanicek and Kramer 1969; USFWS 2002b; D. Ryden 2013, personal communication). BONY develop a slight dorsal keel as adults (USFWS 2002a), which would have discouraged some pikeminnow predation (Portz and Tyus 2004; Franssen et al. 2007). Otherwise, BONY morphology would not have deterred pikeminnow predation. Pikeminnow predation therefore may have shaped the evolution of BONY body form and behaviors, which in turn affect BONY vulnerability to the predators in the system today (see chapters 1 and 3).

BONY larvae, fry, juveniles, and adults use cover for protection, show a preference for night activity, and exhibit defensive behaviors that may help them avoid predators (Mueller 2006; Marsh et al. 2013b; Ward and Figiel 2013). Mobility and agility for avoiding or escaping predators presumably increase with age among juveniles and adults, and body size alone may provide some protection against larger predators (e.g., pikeminnow, see above), at least among adults.

However, these evolved BONY adaptations to predatory pressure may not provide sufficient defense against the non-native predators that now dominate the ecosystem (Karam and Marsh 2010). These non-native predators find the native fishes of the LCR easy targets, as indicated, for example, by their differential consumption of native fishes compared to their consumption of other non-natives (Pilger et al. 2008; Yard et al. 2011). Three sets of observations particularly strongly point to predation by non-native fishes as the major cause – or one of the top causes – of BONY mortality in the present-day system:

(1) BONY remains have been detected in the stomach contents of non-native fishes along the lower and upper Colorado River (Bestgen et al. 2008; Karam and Marsh 2010).

(2) Introductions of non-native piscivorous fishes into isolated ponds along the lower and upper Colorado River previously free or nearly free of piscivorous fishes all result in rapid decimation or elimination of BONY from the affected ponds (Christopherson et al. 2004; Mueller 2005, 2006).

(3) The major, rapid decline of BONY in the LCR in the 1930s followed the introduction of several large non-native piscivorous fishes, specifically channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) (see review of historic literature by Mueller 2005). This decline preceded the period of construction of the major dams along the LCR, which inundated large stretches of former shoreline and backwater wetlands. In fact, BONY numbers in the LCR subsequently initially increased following the filling of Lakes Mohave and Mead (Mueller 2005). Conceivably, the high fecundity of BONY (see chapter 2) allowed them to populate these reservoirs rapidly before the impounded populations of non-native piscivorous fishes caught up: BONY numbers crashed in Lakes Mohave and Mead shortly after their initial resurgences (Mueller 2005).

Human predation on BONY also apparently has a long history along the LCR as indicated by prehistoric remains along the LCR and along the strand lines of former freshwater Lake Cahuilla (Gobalet and Wake 2000; Gobalet et al. 2005).

The lake, an extension or relocation of the LCR into the Salton Basin (California and Baja California, Mexico), formed and receded several times following the Pleistocene, most recently approximately 500 years ago. Large quantities of BONY bones at prehistoric campsites, the presence of BONY bones in human coprolites (fecal fossils), and the remains of hundreds of coeval V- and U-shaped rock weirs at successively descending lake strand lines indicate that the indigenous peoples of the region consumed BONY in large quantities. The weirs are thought to have functioned as traps for schools of fish driven away from lake littoral shallows toward deeper water. The archaeological sites may date to the last period of lake expansion.

Mueller (2006) and Kesner et al. (2008) suggested that changes in water turbidity also have affected rates of predation on BONY. Specifically, they suggested that lower turbidity in the regulated river and isolated ponds of the LCR may increase BONY vulnerability to predation, including by piscivorous birds. BONY sometimes visit (e.g., for spawning) or travel through shallows even in the daytime (Mueller 2006), where they may also be vulnerable to avian predation even in moderately turbid water. No studies have systematically investigated avian predation on BONY, but studies of RASU provide a potential analog. Schooley et al. (2008) studied avian predation on RASU along the LCR in 2003–08 and noted wounds attributable to avian attacks on approximately 23 percent of all RASU captured. The investigators also suggested that, as RASU shifted their typical position downward in the water column with age, avian attacks would become less common. In such circumstances, avian attacks would be limited not simply by depth but by water clarity, limiting the depths to which avian predators could detect their prey.

Hatchery-reared BONY may experience uniquely higher rates of predation due to their lack of experience with predator, and possibly due to patterns of surfacing behavior developed at their rearing facilities, as has been hypothesized for other species (Schooley et al. 2008). Tracking of hatchery-reared BONY released along the LCR into open river and reservoir settings as well as ponds with non-native predators indicate that most or all die within a short few weeks following release, with predation the suspected but unconfirmed leading cause of the mortality (Mueller et al. 2005; Montony 2008; Pacey and Marsh 2008b; Karam et al. 2011, 2012, 2013; Kesner et al. 2010a, 2010b; Mueller et al. 2014). This has led to the hypothesis that pre-conditioning of swimming strength and/or predator recognition might help BONY along the LCR better avoid predators (Lentsch et al. 1995; Nesler et al. 2003; Reclamation 2006; Mueller et al. 2007; Portz 2009; Ward and Figiel 2013). The topic is the subject of ongoing research by and funded through LCR MSCP Work Task C11, Bonytail Rearing Studies (Reclamation 2014) and a topic of broad interest in general (Olson et al. 2012; Archer and Crowl 2014).

RESTING

BONY need to rest to conserve energy during every mobile life stage. They may have specific preferences for the habitat conditions they seek in resting locations that afford them suitable proximity to food resources and protection from predators and thermal, chemical, or mechanical stress, and these preferences may differ among life stages and vary with time of day (USFWS 2002a; Mueller et al. 2003; Christopherson et al. 2004; Mueller 2006, 2007; Reclamation 2008; Kesner et al. 2010a, 2010b; Marsh et al. 2013b). BONY were observed remaining inside cavities in riprap at Cibola High Levee Pond during daylight hours, venturing out only after sunset, and returning to the same cavities just before sunrise (Mueller et al. 2003; Marsh et al. 2013b). Mueller et al. (2003), citing Minckley and Rinne (1985) also noted that rock cavities such as those favored by BONY at Cibola High Levee Pond would have been rare in the basin prior to regulation, but that "… woody debris, large snags, root wads, and drift piles" would have created plentiful similar cavities. Mueller et al. (2003) also noted that "The use of cavities may have been an effective survival strategy to reduce avian predation, but today, with the presence of channel and flathead catfishes, this behavior may put bonytail at greater risk."

The ability of BONY to find and return to suitable resting sites presumably increases as their range of mobility increases with size and age. BONY preferences for resting habitat are a topic of ongoing investigations funded through LCR MSCP Work Tasks C41, Role of Artificial Habitat in Survival of Razorback Sucker and Bonytail; C58, Investigating Shoreline Habitat Cover for Bonytail; and C63, Evaluation of Habitat Features that May Influence Success of Razorback Sucker and Bonytail in Backwater Environments (Reclamation 2014).

SWIMMING

BONY swim to explore, find and position themselves within habitat, avoid hazards, feed, and stage and spawn. Swimming ability first appears among larvae as they approach swim-up, and BONY thereafter develop into stronger, more agile swimmers with greater stamina. Juveniles and older BONY swim over increasingly large distances within and sometimes among river macrohabitats over distances of up to 10 km per day (Mueller 2006). In parts of the Colorado River basin with few dams, they have been observed to travel over 300 km between main stem and tributary settings over timespans of a few months (Bottcher et al. 2013). At least at a local scale, a large proportion of adult BONY shows fidelity to specific resting sites, to which they return after foraging forays (Marsh et al. 2013b). Swimming abilities may be temperature sensitive, at least among younger BONY (Berry and Pimentel 1985) (see "Water Temperature," chapter 4).

BONY sometimes swim in aggregations or "schools." Schooling not associated with spawning first appears among fry and juveniles and has been reported for all subsequent age classes in both hatchery settings and ponds (Hamman 1982; Mueller et al. 2003, 2004; Mueller 2006). Fry and juveniles may form schools of as many as several hundred individuals during the day (Moffett 1943 cited in Mueller 2006; Jonez and Sumner 1954; Mueller 2006), while schools of adults have been observed only at night (Mueller 2006). Mueller (2006) summarized observations that BONY form tight schools in response to the presence of predators, and further noted that BONY "… exhibit a unique startle defense that Chester Figiel (USFWS) termed as 'scrumming,' after the rugby term. Fish form a tight ball with their heads aligned toward the center while they beat their tails rapidly …. The frenzy is believed to be a defensive behavior designed to startle predators. We observed this common hatchery behavior twice at CHLP [Cibola High Levee Pond]."

Juvenile and adult BONY are reportedly highly agile and energetic in trying to avoid hazards such as nets, exhibiting behaviors such as leaping out of floating pens and actively searching for escape routes over, under, around, and through nets (Mueller 2006). Juvenile and adult BONY avoid sunlight, feeding preferentially at night (Lentsch et al. 1995; Mueller 2006; Marsh et al. 2013b). In contrast, light traps are a common tool for attracting BONY larvae for sampling, although this may also expose the larvae to predation (Snyder and Meisner 1997; Mueller 2006). Mueller (2006) also noted that "… Bonytail are easily captured from rearing ponds using recreational angling equipment. However, once a fish is hooked, it then becomes difficult to capture others, suggesting the fish may release fright pheromones (Quent Bradwisch, UDNR, personal communication, 2004)." More broadly, BONY adult morphology suggests an adaptation for strong swimming and/or swimming against strong currents (Minckley 1991; Mueller 2006).

Marsh (1985) also reported a unique pattern of behavior among BONY larvae shortly after to swim-up: "As larvae began actively swimming they moved upward in the water column then ceased motion and sank slowly, head first. Many larvae apparently adhered to sides of incubation chambers with the anteroventral portion of the head contacting the solid surface and the body extending perpendicularly. When such larvae were displaced they performed a directed swimming motion back toward an attachment surface, butting several times until regaining contact. The mechanism of adhesion is as yet unknown."

Swimming abilities among hatchery-reared BONY have received special attention. Temperature affects their swimming strength, as discussed below (see "Water Temperature," chapter 4). Additionally, regardless of temperature, newly released BONY may lack stamina for long-distance movement initially following release and lack strength for avoiding predators (Lentsch et al. 1995; Ward and Hilwig 2004; Mueller et al. 2007; Pacey and Marsh 2008a; Portz 2009; Ward and Figiel 2013) (see "Pre-Release Conditioning" and "Water Flow/Turbulence," chapter 4). The potential benefits of conditioning swimming abilities among reared BONY prior to release are scheduled for investigation under LCR MSCP Work Task C61, Evaluation of Alternative Stocking Methods for Fish Augmentation (Reclamation 2014).

THERMAL STRESS

Exposure to water temperatures outside their range of tolerance—in both natural and artificial environments—render BONY in every life stage vulnerable to altered performance, disease, stress, and mortality (Vanicek and Kramer 1969; Bulkley et al. 1982; Hamman 1982, 1985; Berry and Pimentel 1985; Marsh 1985; USFWS 2002a; Mueller 2006; Ward 2006; Bestgen et al. 2007a, 2008; Pacey and Marsh 2008a; Portz 2009; Sykes 2011; Kappenman et al. 2012). 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, including scientific capture and handling (Ward 2006; Hunt et al. 2012). However, as BONY mature, they become increasingly able to avoid or escape settings in which they may sense thermally unsuitable conditions – if these conditions permit such avoidance or escape. This can pose a challenge, however, when BONY 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 17 habitat elements that affect 1 or more critical biological activities or processes across the 5 BONY life stages. Some of these habitat elements differ in their details among life stages. For example, different BONY life stages experience different taxa, sizes, and densities of invertebrate, aquatic vertebrate, and avian and mammalian predators. However, using the same labels for the same *kinds* of habitat elements across all life stages makes it easier to compare and integrate the CEM for each life stage into a single overarching CEM. Table 3 lists the 17 habitat elements and the critical biological activities and processes that they *directly* affect across all BONY life stages.

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

Critical activity or process ➔ **➔ Habitat element**	Chemical stress	Competition	Disease	Drifting	Egg settling and adhesion	Foraging	Mechanical stress	Predation	Resting	Swimming	Thermal stress
Aquatic macrophytes						X		X	X	X	
Aquatic vertebrates		X				X		X			
Birds and mammals		X						X			
Fishing encounters							X				
Infectious agents			X								
Invertebrates and particulate organic matter	X	X				X		X			
Macrohabitat geometry				X						X	
Mesohabitat geometry/cover				X		X		X	X	X	
Post-rearing transport and release methods	X						X				X
Pre-release conditioning	X		X			X		X	X	X	X
Scientific study					X		X				
Substrate texture/dynamics					X		X		X		
Turbidity						X		X	X	X	
Water chemistry	X								X	X	
Water depth							X				
Water flow/turbulence				X	X		X		X	X	
Water temperature	X								X	X	X

The diagrams and other references to habitat elements elsewhere in this document identify the habitat elements by a one-to-three-word short name. However, each short name refers to a longer, complete name. For example, the habitat element label, "aquatic vertebrates," is the short name for "the taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of aquatic vertebrates that may interact with BONY or its habitat along the LCR, its connected backwaters, and its isolated ponds." The following paragraphs below provide the full name for each habitat element and provide a detailed definition, addressing the elements in alphabetical order.

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.)

AQUATIC MACROPHYTES

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

The species listed in table 4 and detritus from them may provide cover and food for BONY; cover, food, and habitat for invertebrates and small aquatic vertebrates that may in turn become food for BONY; and habitat for aquatic invertebrates and vertebrates that may prey on or compete with BONY in different life stages (Mueller 2006) (see "Competition," "Foraging," "Predation," and "Resting," chapter 3). For example, overly dense stands of aquatic macrophytes, such as giant salvinia, may suppress aquatic invertebrate abundance by reducing light and DO levels (NISIC 2014).

Historically, the types, abundance, and distribution of aquatic macrophytes along the LCR and its backwaters depended on the availability of at least relatively stable shoreline and backwater shallows (Johnson 1991). Aquatic macrophytes in these settings in fact may help sustain their own habitat by stabilizing substrates and slowing the movement of water (Carlson et al. 1979; Fernandez and Madsen 2013). Shallow backwaters, embayments, and tributary confluences continue to support aquatic macrophytes along the LCR (Karam et al. 2011, 2012, 2013; Fernandez and Madsen 2013). However, river regulation and flood plain development have greatly reduced the availability of these mesohabitat types. At the same time, the highly invasive giant salvinia is spreading in the LCR ecosystem (NISIC 2014). One or more possibly non-native varieties of common

Table 4.—Aquatic macrophytes of the LCR

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

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

reed (*Phragmites australis*) (Saltonstall 2002) also may now occur, contributing to the spread of common reed throughout the LCR ecosystem. These changes to the aquatic macrophyte assemblage along the LCR will have as-yet unknown ecological consequences (McFarland et al. 2004; Rogalski and Skelly 2012).

AQUATIC VERTEBRATES

***Full name*: The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of aquatic vertebrates that may interact with BONY or its habitat along the LCR, its connected backwaters, and its isolated ponds.** Interactions may include predation on, competition with, or serving as food items for BONY. Most of these vertebrates are native and non-native fishes. The assemblage also includes one amphibian (e.g., bullfrog [*Rana catesbeiana*]) and their larvae (*aka* tadpoles), following Mueller (2006, 2007) and Mueller et al. (2006). Activity levels may vary in response to other habitat conditions (e.g., water temperature and water quality).

Table 5 lists all aquatic vertebrates reported in the present-day LCR (Ohmart et al. 1988; Minckley 1991; Mueller and Marsh 2002; Minckley et al. 2003; Gobalet et al. 2005; Marsh and Pacey 2005; Minckley et al. 2003; U.S. Geological Survey [USGS] Nonindigenous Aquatic Species Program [http://nas.er.usgs.gov/]). Table 5 also identifies whether each species is native (N), introduced as a sport fish (S), introduced as bait or forage for sport fish (B), or other. "Other" includes accidental introductions such as the bullfrog, which arrived merely by escaping (NISIC 2014).

Miller (1952), Mueller and Marsh (2002), and others list other species historically introduced into the LCR prior to 1975. However, more recent records indicate that these additional species no longer occur in the LCR, and table 5 therefore omits them.

Table 5 identifies those species that the literature explicitly recognizes or proposes as predators on BONY based on studies at Cibola High Levee Pond in the Cibola National Wildlife Refuge (Mueller 2006, 2007; Mueller et al. 2006), in Lake Mohave (Bozek et al. 1984; Karam and Marsh 2010; Karam et al. 2011, 2012, 2013), and in the UCRB (Joseph et al. 1977; Christopherson et al. 2004; Brunson and Christopherson 2005; Bestgen et al. 2006). Published evidence of aquatic vertebrate predation on BONY otherwise is rare. However, such predation is widely thought to be a major cause of BONY population declines and the failure of stocked BONY to survive outside of hatcheries and isolated ponds.

Table 5 also identifies aquatic vertebrates that have ecological characteristics suggesting they could prey on BONY or ecological characteristics suggesting their juveniles or adults could compete with BONY for food items or physical habitat. The information on ecological characteristics suggesting the possibility of predation or competition comes from the FishBase (Froese and Pauly 2014) and NatureServe Explorer (NatureServe 2014) databases. The large number of entries in table 5 for possible competition reflects the fact that BONY are omnivorous (see Foraging," chapter 3). This puts them in potential competition with numerous aquatic omnivores, herbivores, insectivores, crustacivores, and piscivores. The search of these databases considered only reported ranges of food items, not feeding habitats, behaviors, or schedules.

Table 5.—Aquatic freshwater vertebrates of the LCR

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

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

BONY feed on some of the species listed in table 5 (Marsh and Schooley 2004; Marsh et al. 2013a). For example, Marsh et al. (2013a) found that the stomach contents of larger BONY (> 400 mm TL) at Cibola High Levee Pond consistently included fish remains, and they specifically report BONY consuming bullfrog larvae and western mosquitofish. BONY also consume their own eggs (Mueller 2006) and compete for limited cover opportunities in crowded settings (Mueller 2006; Marsh et al. 2013b).

BIRDS AND MAMMALS

***Full name*: The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the bird and mammal assemblages.** This element refers to the range of bird and mammal species known or suspected to interact with BONY or its habitat along the LCR, its connected backwaters, and its isolated ponds. More precisely, the list of species consists of birds and mammals, known or suspected to prey on BONY when the fish approach the water surface or shoreline, and beaver (*Castor canadensis*), which create meso- and microhabitats beneficial to BONY. Mueller (2006) observed or suspected predation on BONY at Cibola High Levee Pond by “kingfishers, osprey, cormorants, pelicans, … night herons, and great blue herons;” and by “… raccoons, ringtail cats (*Bassariscus astutus*), and other fish-eating animals.” Kesner et al. (2008) similarly strongly suspected “… Double-crested Cormorant *Phalacrocorax auritus* and American white pelican *Pelecanus erythrorhynchos*” as significant predators on BONY at Imperial Ponds. Mueller et al. (2014) summarized other reports of observed or suspected significant avian predation on BONY along the LCR. An analogy with RASU suggests that coyotes (*Canis latrans*) may also prey on BONY when they approach the shoreline (Mueller 2006).

In turn, Mueller (2006) recorded significant interactions of beaver with BONY at Cibola High Levee Pond that suggested a historic commensal relationship. Specifically, BONY spawned on a patch of substrate cleared of fine sediment by beaver activity, and “Small bonytail were routinely found in the entrances of flooded beaver dens.” The overhangs of the den entrances apparently provided the small BONY with dark cavities for cover. Beaver also eat aquatic macrophytes, and thereby may shape their availability and generate particulate organic matter at the same time (Henker 2009).

FISHING ENCOUNTERS

***Full name*: The frequency and intensity with which BONY are caught by recreational fishers.** BONY reportedly can be taken readily with a baited hook, and recreational anglers occasionally catch them along the LCR main stem and in its reservoirs (Minckley 1991; USFWS 1990, 2002a; Mueller 2006; Minckley and Thorson 2007; Karam and Marsh 2010; Karam et al. 2011, 2012, 2013; Wolff et al. 2012). Encounters between anglers and BONY are rare along the LCR today because BONY are so rare. Nevertheless, the CEM recognizes that this habitat element could potentially affect BONY recovery.

INFECTIOUS AGENTS

***Full name*: The types, abundance, distribution, and activity of infectious agents.** As noted above (see "Disease," chapter 3), BONY in every life stage are vulnerable to infection. Non-lethal infections may make the affected individuals vulnerable to mortality from other causes. "Infectious agents" refers to the spectrum of viruses, bacteria, fungi, and parasites present and capable of infecting BONY in the open environment of the LCR, including anchor worms (*Lernea* spp.), ich (*Ichthyophthirius multifilis*), and the Asian tapeworm (*Bothriocephalus acheilognathi*) (Flagg 1982; Hamman 1982; Bozek et al. 1984; Marsh 1985; Tyus et al. 1999; Hansen et al. 2006, 2007; Mueller 2006; Bestgen et al. 2008; Pacey and Marsh 2008a; Portz 2009; Archdeacon et al. 2010; Sykes 2011; Linder et al. 2012; Marsh et al. 2013a).

The risk of infection presumably increases with the diversity and abundance of such agents, the spatial extent of their distribution, the effects of water conditions (e.g., temperature) on their activity, and the presence of other species as carriers. BONY freshly released from hatcheries or from scientific handling in the field also appear particularly vulnerable (Pacey and Marsh 2008b; Sykes 2011; Mueller et al. 2014). The CEM does not address BONY rearing in hatcheries, which have their own concerns about disease (Ward et al. 2007; Pacey and Marsh 2008a). However, the knowledge obtained from these controlled environments does contribute to the understanding of disease among BONY in the open environment of the LCR and its off-channel environments.

INVERTEBRATES AND PARTICULATE ORGANIC MATTER

***Full name*: The taxonomic, functional, and size composition; abundance; spatial and temporal distributions; activity level of the invertebrate assemblage; and the abundance and nutritional quality of particulate organic matter.** The invertebrates covered by this element consist of biofilms, phyto- and zooplankton; aquatic macroinvertebrates of the water column and benthos, including insect larvae, crayfish, and small bivalves; and terrestrial insects that fall or land on the water. Particulate organic matter consists of plant litter and other decomposing organic matter carried into BONY habitat by tributary inflows, litter dropped directly into the water from overhanging vegetation, and the decomposing remains of other aquatic organisms. As noted in the full name, the habitat element refers to the taxonomic composition of the invertebrate assemblage; the functional composition of the invertebrate assemblage, including feeding guilds and nutritional value; the size(s); abundance; and spatial and temporal distributions of the invertebrates; and their level of activity as it varies with other habitat conditions (e.g., water temperature and turbidity). As also noted in the full name, this habitat element refers to both the abundance and nutritional quality of the particulate organic matter.

BONY feed on terrestrial and aquatic invertebrates and particulate organic matter but prefer different sizes and types of these food items during different life stages. The assemblage of aquatic invertebrates also includes some species, such as crayfish, and certain kinds of insect larvae, which prey on larval and early juvenile BONY (Horn et al. 1994; Mueller 2006; Mueller et al. 2006) and also compete with them for food (particulate organic matter and smaller aquatic invertebrates). However, BONY also feed on these same invertebrates; adult BONY predation on crayfish appeared to help control crayfish numbers at Cibola High Levee Pond (Mueller 2006), significantly reducing their predation on BONY and RASU eggs.

Two species of non-native crayfish occur in BONY habitat: the virile or northern crayfish (*Orconetes virilis*) and the red swamp crayfish (*Procambarus clarkii*). Non-native filter-feeding bivalves such as the Asian clam (*Corbicula fluminea*), quagga mussel (*Dreissena rostriformis bugensis*), and zebra mussel (*Dreissena polymorpha*) compete with BONY for plankton and floating detritus and may blanket benthic habitat, although BONY may also feed on these same species (Lenon et al. 2002; Mueller 2006; Nalepa 2010; Martinez 2012; Marsh et al. 2013a). Blooms of the non-native golden alga (*Prymnesium parvum*) produce a toxin harmful to BONY and many other fishes, although these blooms occur only under special circumstances (Baker et al. 2009; Brooks et al. 2011; Roelke et al. 2011).

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

MACROHABITAT GEOMETRY

***Full name*: The types, abundance, and spatial and temporal distributions of aquatic macrohabitats.** This element refers to the large-scale (i.e., 1–100 km scale) shape of the river channel, backwaters and other off-channel wetted areas, and the connected flood plain as well as the distribution of specific aquatic macrohabitat types. Scattered observations along the upper and lower Colorado River and its tributaries suggest that adult BONY occupied main stem and tributary river reaches in canyons, reaches with adjacent flood plain, and backwaters with depths of 1–10 m and moderate flow with low turbulence, and they spawned on shoals within these same macrohabitat types (Holden 1973; Holden and Stalnaker 1975; Smith et al. 1979; Bozek et al. 1984; Kaeding et al. 1986; Minckley 1991; Marsh and Mueller 1999; Mueller and Marsh 2002; USFWS 2002a; Christopherson et al. 2004; Brunson and Christopherson 2005; Modde and Haines 2005; Reclamation 2005, 2008; Bestgen et al. 2006, 2007a, 2008; Mueller 2006, 2007; Minckley and Thorson 2007; Pacey and Marsh 2008b; Valdez et al. 2011; Bottcher et al. 2013; Mueller et al. 2014). The type specimen for the species was collected on the Zuni River, a small tributary to the Little Colorado River that arises in the Zuni Mountains along the Continental Divide (USFWS 2002a). At the other extreme, Mueller (2006) proposed that BONY historic habitat also included the Colorado River Delta.

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 (Reclamation 2004). 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. At present, 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, macrohabitat geometry today depends on the design and operation of the main stem water storage-delivery system, tributary inflow, and pond, channel, and shoreline management. Ongoing research addresses the topic of BONY macrohabitat associations through LCR MSCP Work Tasks C39, Post-Stocking Distribution and Survival of Bonytail in Reach 3; C49, Investigations of

Razorback Sucker and Bonytail Movements and Habitat Use Downstream from Parker Dam; and C64, Post-Stocking Movement, Distribution, and Habitat Use of Razorback Sucker and Bonytail (Reclamation 2014).

MESOHABITAT GEOMETRY/COVER

***Full name*: The types, abundance, and spatial and temporal distributions of aquatic mesohabitats and cover provided by these habitats.** This element refers to a finer-scale (i.e., site scale) of aquatic habitat variation along the river channel, its backwaters, and its isolated ponds. Mesohabitats are portions of macrohabitats that vary in depth, flow velocity and turbulence, substrate size and shape, aquatic vegetation, and/or proximity to other mesohabitats. Fish behavior often varies strongly with mesohabitat setting (Parasiewicz et al. 2008), and mesohabitat arrangements may affect drift path geometry.

Examples of river mesohabitat types include bars, eddies, nearshore slackwaters, pools, riffles, and runs. As noted earlier (see “Drifting,” chapter 3), channel sections along which lateral and reverse currents draw drifting fry out of the main line of downstream flow into low-velocity settings constitute a type of mesohabitat. This document suggests referring to such settings as “interception habitat,” following terminology developed for a CEM for the endangered pallid sturgeon, to support species recovery along the Missouri River (W. Nelson-Stastny 2015, personal communication). However, the literature on mesohabitats and native fish ecology along the Colorado River does not yet use this term.

Scattered historic and recent observations along the upper and lower Colorado River, its tributaries, and isolated backwaters record the presence of BONY in a range of mesohabitats during different life stages and during different times of the day. However, few investigators gave close attention to BONY use of different mesohabitats prior to the collapse of the species across the upper and lower basins. In turn, BONY mesohabitat use today is rarely closely observed outside of artificial settings. As a result, the literature records only a handful of potential associations between BONY life stages and particular mesohabitat or cover types:

- BONY fry and juveniles are thought to seek out backwaters or inundated flood plain wetlands as rearing habitat (USFWS 2002a; Christopherson et al. 2004; Brunson and Christopherson 2005; Modde and Haines 2005; Reclamation 2005, 2008). Given the limited swimming ability of BONY fry, and consequently the dominance of drift in transporting the fry from their natal sites to suitable rearing habitat, the availability and spatial arrangement of interception habitat along the drift path likely also affected the ability of BONY fry to successfully encounter and move into rearing habitat.

- Adults in riverine settings, and juveniles following their departure from wild rearing habitats, appear to prefer swift runs and riffles, point bars, and pools and eddies adjacent to swift currents in main channels (Joseph et al. 1977; Valdez and Clemmer 1982; Bozek et al. 1984; Kaeding et al. 1986; USFWS 2002a; Reclamation 2005, 2008; Bestgen et al. 2006; Minckley and Thorson 2007; Bestgen et al. 2008). These reported settings vary widely in total depth, and BONY move throughout the water column in these settings. Minckley (1991), for example, described BONY moving up and down in mid-channel between near-surface, mid-water, and bottom depths seeking food.

- Reports of juveniles and adults in impoundments, including isolated ponds, note that BONY concentrate during the day in settings that provide dense cover, such as submerged and emergent vegetation (Karam et al. 2011, 2012, 2013), or riprap with cavities into which the fish insert themselves apparently to avoid predators (Marsh and Mueller 1999; Mueller 2006; Marsh et al. 2013a), moving into open water to feed at night.

- BONY spawning has been observed in reservoirs over "gravel shelves" at depths up to 10 m (Bozek et al. 1984) and in isolated ponds over near-shore gravel shallows with as little as 0.5 m depth but adjacent to deeper water (Mueller 2006). Gobalet and Wake (2000) presented evidence of native American use of stone weirs to trap spawning BONY along gravel shores of ancient Lake Cahuilla, Salton Basin, an episodically inundated tributary to the Colorado River Delta.

Mesohabitat geometry, including provision of cover for BONY, historically was shaped by the same factors that shaped macrohabitat geometry but at a finer spatial scale. These factors include main stem and tributary riverflows and their loads of sediment and snags interacting with river and flood plain vegetation and geology. Mesohabitat geometry similar to historic conditions currently occurs along the LCR only in a few places where the channel is confined by bedrock and at tributary confluences. Otherwise, today, mesohabitat geometry along the LCR depends on the design and operations of the main stem water storage-delivery system; tributary inflow; pond, channel, and shoreline management; and the effects of submerged and emergent vegetation and macrohabitat geometry. Dams have eliminated almost all inputs of sediment and large woody debris (Minckley and Rinne 1985) from the upper to the lower Colorado River and from one LCR reach to the next. For example, BONY use the interstices created by levee riprap as cover at Cibola High Levee Pond (Mueller 2006) as a substitute for presumed natural cover types such as bank overhangs, interstices in benthic gravels, bedrock crevices, and pockets beneath large woody debris (Marsh et al. 2013b). Ongoing research addresses the topic of BONY mesohabitat associations through LCR MSCP Work Tasks C25, Imperial Ponds Native Fish Research; C39, Post-Stocking Distribution and Survival of Bonytail in Reach 3; C41, Role of Artificial

Habitat in Survival of Razorback Sucker and Bonytail; C49, Investigations of Razorback Sucker and Bonytail Movements and Habitat Use Downstream from Parker Dam; C58, Investigating Shoreline Habitat Cover for Bonytail; and C64, Post-Stocking Movement, Distribution, and Habitat Use of Razorback Sucker and Bonytail (Reclamation 2014).

POST-REARING TRANSPORT AND RELEASE METHODS

***Full name*: The methods used to transport and release hatchery-reared BONY.** This element refers to the methods by which BONY are collected, size-selected, and transported from hatcheries for release into the LCR main stem and reservoirs, backwaters, and isolated ponds; the types of locations and times of day and year during which they are released; and whether they are tagged during this process for tracking following release. Some or all of these variables may affect BONY survival following release (e.g., by causing them physiological stress or releasing them into settings that reduce their ability to survive) (Marsh and Mueller 1999; Sowka and Brunkow 1999; USFWS 2002a; Mueller et al. 2003, 2004, 2005; Nesler et al. 2003; Mueller 2006, 2007; Reclamation 2006; Minckley and Thorson 2007; Bestgen et al. 2008; Kesner et al. 2008, 2010a, 2010b; Montony 2008; Pacey and Marsh 2008a, 2008b; Portz 2009; Karam and Marsh 2010; Karam et al. 2011, 2012, 2013; Sykes 2011, 2013; Mueller et al. 2014). Ongoing research addresses the topic of post-rearing transport and release through LCR MSCP Work Tasks C39, Post-Stocking Distribution and Survival of Bonytail in Reach 3; C46, Physiological Response in BONY and RASU to Transport Stress; C63, Evaluation of Habitat Features that May Influence Success of Razorback Sucker and Bonytail in Backwater Environments; and C65, Evaluation of Immediate Post-Stocking Survival of Razorback Sucker and Bonytail (Reclamation 2014).

PRE-RELEASE CONDITIONING

***Full name*: The types and extent of pre-release conditioning of reared BONY physiology and behavior.** This element refers to the pre-release conditioning of reared BONY to the range of environmental conditions they will encounter upon release, including flow velocities, water temperatures, habitat types, food items, infectious agents, and predator attention/attacks. A growing literature proposes or indicates that such conditioning can increase survival among repatriated fishes, including BONY (Lentsch et al. 1995; Ward and Hilwig 2004; Reclamation 2006; Mueller 2007; Mueller et al. 2007; Bestgen et al. 2008; Pacey and Marsh 2008; Portz 2009; Ward and Figiel 2013) (see “Water Flow/Turbulence,” this chapter). The potential benefits of conditioning swimming abilities among reared

BONY prior to release are scheduled for investigation under LCR MSCP Work Task C61, Evaluation of Alternative Stocking Methods for Fish Augmentation (Reclamation 2014) and is a topic of broad interest in general (Olson et al. 2012; Archer and Crowl 2014).

SCIENTIFIC STUDY

***Full name*: The types, frequencies, and duration of scientific monitoring, capture, and handling.** This element refers to the possibility of capture, examination, tagging, removal, and experimental treatment of BONY during scientific studies focused on the LCR, its backwaters, and its isolated ponds. This element does not refer to the scientific study of BONY at hatcheries or rearing facilities. Detection and capture methods and their associated sampling designs vary in their suitability for different mesohabitats, in their likelihood of encountering BONY of different sizes and life stages, and in their effects on captured individuals (Tyus et al. 1999; Mueller et al. 2004, 2005; Paukert et al. 2005; Mueller 2006, 2007; Ward 2006; Bestgen et al. 2008; Kesner et al 2008, 2010a, 2010b; Montony 2008; Pacey and Marsh 2008b; Ward et al. 2008; Portz 2009; Karam et al. 2011, 2012, 2013; Dowling et al. 2011; Hunt et al. 2012). BONY appear to be particularly vulnerable to stress during capture and handling (Tyus et al. 1999; Paukert et al. 2005; Mueller 2006; Montony 2008; Pacey and Marsh 2008a; Portz 2009). For example, Mueller (2006) provided a detailed discussion of the frequent incidence of ruptured muscle syndrome among BONY captured by netting at Cibola High Levee Pond, leading to death, which he equated with capture myopathy (Spraker 1993).

SUBSTRATE TEXTURE/DYNAMICS

***Full name*: The abundance, spatial distributions, and stability of substrate types (textures).** This element refers to particle size distribution and embeddedness and the interstitial cavity size distribution of benthic sediment within mesohabitats; substrate dynamics such as the frequency of shifting, scour, and burial; and other potentially important features of the substrate. These features may affect substrate suitability for BONY spawning, nursery, resting, or foraging.

Scattered historic and recent observations along the upper and lower Colorado River, its tributaries, and isolated backwaters record the presence of BONY over a variety of substrates during different life stages and during different times of the day. However, few investigators gave close attention to BONY associations with different substrates prior to the collapse of the species across the upper and lower basins. In turn, BONY occurrence over different substrates today is rarely closely observed outside of artificial settings. As a result, the literature records only a handful of consistent associations between BONY life stages and particular substrates:

- Adults in riverine settings, and juveniles following their departure from wild rearing habitats, appear to prefer sand, coarse gravel, boulder, or hard substrates (Valdez and Clemmer 1982; Bozek et al. 1984; Kaeding et al. 1986; Bissonette and Crowl 1995, cited in Lentsch et al. 1995; USFWS 2002a; Reclamation 2005, 2008; Bestgen et al. 2006, 2008). Both adults and juveniles also use cavities or crevices among cobbles, boulders, and riprap as shelter from predators (March and Mueller 1999; Mueller 2006; Marsh et al. 2013a). There is an ongoing program under the LCR MSCP to investigate potential artificial habitat types for BONY in Davis Cove, a 2.7-acre backwater pond along Lake Mohave (LCR MSCP Work Task C41, Role of Artificial Habitat in Survival of Razorback Sucker and Bonytail). In October 2011, young-of-year BONY were discovered residing inside polyvinyl chloride pipe (size not specified) that had been introduced into the pond as the frame for an experimental brush habitat (Reclamation 2014).

- As noted above (see "Mesohabitat Geometry/Cover," this chapter), BONY have been observed spawning over "gravel" substrates in reservoirs (Bozek et al. 1984) and isolated ponds (Mueller 2006). Mueller (2006) specifically defined the spawning gravels at Cibola High Levee Pond as uniformly 2–4 centimeters in diameter, which corresponds to "coarse" to "very coarse" pebbles in the Wentworth system of particle size classification (Williams et al. 2006). Mueller (2006) further noted that BONY spawn over "clean" substrates (i.e., substrates cleaned or kept free of fine particles by water currents, beaver activity, or "finning" by the spawning adults). Broadcast eggs settle into the clean(ed) interstices among the pebbles, which may at least partially protect them from predators (see "Egg Settling and Adhesion," chapter 3).

Unfortunately, the literature does not indicate what particular features of substrates make them attractive to BONY other than as matrixes of protective crevices and cavities. For example, no evidence is available to determine whether BONY seek out settings with specific substrates over which to feed. Further, studies of BONY habitat only rarely (Mueller 2006) provide quantitative or standardized qualitative descriptions of substrate texture suitable for comparison among field studies. Such quantitative or standardized qualitative descriptions of substrate texture are crucial for identifying statistical preferences in fish habitat use (Quist et al. 2005; Hightower et al. 2012). Finally, field studies provide no information on the relative stability of substrates used (versus not used) by BONY in any life stage other than indicating that the species prefers "clean" substrates for spawning. Ongoing research addresses the topic of BONY substrate associations through LCR MSCP Work Tasks C41, Role of Artificial Habitat in

Survival of Razorback Sucker and Bonytail; C58, Investigating Shoreline Habitat Cover for Bonytail; and C63, Evaluation of Habitat Features that May Influence Success of Razorback Sucker and Bonytail in Backwater Environments (Reclamation 2014).

TURBIDITY

***Full name*: The magnitude and spatial and temporal distributions of turbidity.** This element refers to the turbidity at sites potentially used by BONY in each life stage, including the way that turbidity may vary over time. Turbidity for eggs and early larvae refers to conditions only at the spawning sites themselves. The LCR main stem was a turbid environment prior to river regulation, as would have been its connected backwaters during and immediately following inundation during flood pulses, with lower turbidity during low-flow conditions, especially along channel margins and in off-channel settings (Minckley 1991; National Research Council [NRC] 1991, 1999; USFWS 2002a). BONY evolved in this environment, and turbidity therefore is presumed to affect several critical BONY behaviors such as navigating to and from sites for spawning, resting, and foraging; avoiding mechanical stress during flood pulses; and avoiding predators (Smith et al. 1979; Tyus and Minckley 1988; USFWS 2002a; Modde and Haines 2005; Bestgen et al. 2006; Mueller 2006; Kesner et al. 2008; Pacey and Marsh 2008b; Reclamation 2008; Karam et al. 2011, 2012, 2013; Marsh et al. 2013b). Primary productivity (see “Invertebrates and Particulate Organic Matter,” chapter 3) and competitor and predator behaviors vary with turbidity levels due to its effects on light penetration and sighting distances; capture success in field sampling of BONY also varies with turbidity, and many non-native fishes avoid levels of turbidity that native fishes such as BONY readily tolerate (Paulson et al. 1980; Bestgen et al. 2006). The effects of turbidity on BONY survival and non-native fish behavior therefore are the subject of ongoing research interest (Mueller 2007; Valdez et al. 2011; Mueller et al. 2014).

Historically, turbidity along the LCR and its off-channel habitats varied over time and space as a result of variation in main stem and tributary flows, channel and backwater geometry, and main stem and tributary sediment loads. Turbidity levels and their variation in the modern river depend on the trapping of sediment behind dams, regulated flow rates and turbulence, tributary inflows, channel and shoreline management (Reclamation 2004), nuisance species introduction and management, and (in a feedback relationship) planktonic and benthic (periphyton) productivity. The effects involving nuisance species arise because these species include introduced algae, which may create blooms, as well as benthic filter-feeders such as quagga and zebra mussels that filter out large amounts of plankton and particulate organic matter. Introduced benthic feeders such as carp also can cause a 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 magnitudes and horizontal, vertical, and temporal distributions of water chemistry parameters that affect BONY.** This element refers to the water chemistry at sites potentially used by BONY in each life stage, including the ways in which water chemistry may vary over time and space. The element covers parameters such as DO, pH, salinity, naturally occurring dissolved substances, and contaminants such as added nitrate/nitrite, perchlorate, selenium, and artificial organic compounds (Reclamation 2004, 2005, 2010, 2011b, 2011c; Turner et al. 2011; Stolberg 2009, 2012).

BONY during different life stages are known or suspected to be vulnerable to alterations to water chemistry either directly or through the accumulation of contaminants in invertebrates and vertebrates on which BONY feed (Bulkley et al. 1982; Pimentel and Bulkley 1983; Buhl and Hamilton 1996; Buhl 1997; Canton 1999; USFWS 2002a; Hamilton 2003; Tomasso et al. 2003; Dwyer et al. 2005; Mueller 2007; Pacey and Marsh 2008a; Walker et al. 2009). Alterations to dissolved nutrient concentrations along the LCR also affect primary productivity, which in turn affects turbidity; 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 system operations affect water chemistry along the river and its reservoirs through their effects on reservoir operations and releases, and channel, lake, and pond design and operations affect water chemistry through the selection of water sources and water levels in isolated ponds (see below). Numerous habitat elements affect water chemistry, particularly depth and temperature. Ongoing research addresses the topic of water chemistry in isolated ponds and its effects on BONY through LCR MSCP Work Tasks C25, Imperial Ponds Native Fish Research; C32, Determination of Salinity, Temperature, pH, and Oxygen Limits for Bonytail and Razorback Sucker; and C59, Selenium Monitoring in Created Backwater and Marsh Habitat (Reclamation 2014).

WATER DEPTH

***Full name*: The spatial and temporal distributions of water depth.** This element refers to the depth of water covering the habitat sites potentially used or avoided by BONY in each life stage and the ways in which depths vary over time and space. Depth may directly affect site suitability for spawning, resting, foraging, swimming between habitats, and avoiding predation or capture by sampling equipment, or it may indirectly affect these conditions through its effects on other habitat elements such as water temperature or chemistry, flow velocities, or the invertebrate biological community.

Scattered historic and recent observations along the upper and lower Colorado River, its tributaries, and isolated backwaters provide information on BONY use of different depths during different life stages, different activities, or different times of the day. However, few investigators gave close attention to BONY associations with different depths prior to the collapse of the species across the upper and lower basins. In turn, BONY use of different depths today is rarely closely observed outside of artificial settings. As a result, the literature records only a handful of consistent – although often merely qualitative – associations between BONY life stages and particular depths or ranges of depths:

- Brunson and Christopherson (2005) maintained depths of 0.6 m in experimental wetland enclosures to assess the value of flood plain wetlands as rearing habitat for BONY and RASU and noted that larva would have thrived under these conditions but for the effects of intensive predation by non-native fishes.

- Adults in riverine settings, and juveniles following their departure from wild rearing habitats, appear to hover and feed in water characterized as "shallow" (< 2 m) (Bozek et al. 1984) to "deep" (> 10 m) (Minckley 1991). They reportedly move throughout the water column but are found most often at "mid-water" or "near-surface" depths (Minckley 1991).

- Adults and juveniles in impoundments, including isolated ponds, move vertically over the course of the day, hiding in cover during the day and moving into open water at night (Marsh and Mueller 1999; Mueller 2006; Marsh et al. 2013a). Karam et al. (2012) used telemetric data to assess the positioning of stocked BONY in Lake Havasu. They determined that these adults, on average, concentrated their activities at approximately 80 percent of the total height of the water column (as measured from the bottom of the water column) regardless of substrate or absolute depth, but moved higher during twilight and at night.

- Gorman and VanHoosen (2000) found that BONY juveniles from rearing ponds tended to stay near the bottom of the water column in cold (12 °C) water, but moved somewhat more widely in moderately cool (18 °C) water, and moved freely throughout the water column in warm (24 °C) water.

Water depths depend almost entirely on operational decisions at the dams above and/or at intakes and pumps used to control pond levels (see chapter 5). Ongoing research may address the topic of water depth associations for BONY through LCR MSCP Work Tasks C25, Imperial Ponds Native Fish Research; C39, Post-Stocking Distribution and Survival of Bonytail in Reach 3; C41, Role of Artificial Habitat in Survival of Razorback Sucker and Bonytail; C49, Investigations of Razorback Sucker and Bonytail Movements and Habitat Use Downstream from Parker Dam; C58, Investigating Shoreline Habitat Cover for Bonytail; and C64, Post-Stocking Movement, Distribution, and Habitat Use of Razorback Sucker and Bonytail (Reclamation 2014).

WATER FLOW/TURBULENCE

***Full name*: The magnitudes and horizontal, vertical, and temporal distributions of water flow velocity and turbulence.** This element refers to the range of water flow velocities and turbulence encountered by BONY in each life stage. Flow velocity and turbulence may directly affect numerous critical BONY activities and processes during various life stages such as drifting, swimming, and possibly the selection of spawning sites. Additionally, flow velocity and turbulence may affect BONY indirectly through their effects on other habitat elements such as substrate texture/dynamics, turbidity, and mesohabitat geometry (see above, this chapter).

Inundated flood plain wetlands identified as potential BONY larval rearing habitat are low-velocity environments, as would be expected given their hydrology (Lentsch et al. 1995; Christopherson et al. 2004; Brunson and Christopherson 2005). A small number of investigations showed older BONY swimming in flows of varying magnitude along river channels in both the upper and lower basins. These observations often place BONY adults and juveniles in or immediately adjacent to "swift" currents (Joseph et al. 1977; Valdez and Clemmer 1982; Kaeding et al. 1986; Minckley 1991; USFWS 2002a; Reclamation 2005, 2008). However, quantitative measurements of flow velocities used (or avoided) by BONY in either backwater or channel settings are scarce. Few investigators gave close attention to BONY associations with different flow velocities prior to the collapse of the species across the upper and lower basins, and BONY use or avoidance of different flow velocities today is rarely closely observed outside of artificial settings. Bestgen et al. (2006) provided one of the few quantitative field observations of flows associated with BONY, recording stocked adults feeding in runs and riffles along the Green River at "swift" flows > 70 centimeters per second (cm/s).

Laboratory studies have assessed the range of flow velocities against which BONY can swim (not necessarily against which they *prefer* to swim) at different water temperatures versus without prior exercise conditioning:

- Bulkley et al. (1982) found that late-juvenile BONY exhibited sustained swimming speeds of 57 cm/s at 20 °C. This speed exceeded that exhibited by similarly sized RASU and Colorado pikeminnow but not that exhibited by similarly sized humpback chub. The investigators also found that BONY took an average of less than 1 minute to become fatigued in an artificial current at 57 cm/s at 14 °C but an average of more than 60 minutes to become fatigued in this same strength of current at both 20 and 26 °C. Similarly sized RASU, Colorado pikeminnow, and humpback chub became fatigued more quickly at this velocity at all three temperatures.

- Berry and Pimentel (1985) assessed the fatigue velocity (FV_{50}, the velocity at which 50 percent of all individuals failed to continue swimming against a controlled current during tests of 120 minutes duration) of BONY, ≈ 100 mm TL, at 14, 20, and 26°C. FV_{50} averaged 47 cm/s at 14 °C, 50 cm/s at 20 °C, and 52 cm/s at 26 °C, exceeding the performance of similarly sized humpback chub and Colorado pikeminnow.

- Bissonette and Crowl (1995, cited in Lentsch et al. 1995) found that 1-year-old BONY preferred velocities of 6 cm/s.

- Ward and Hilwig (2004) compared the swimming failure velocity at 22 °C of: (a) tank-reared late-juvenile BONY held in standing water, (b) tank-reared late-juvenile BONY conditioned by exercise in water flowing at 10–100 cm/s for > 10 days, and (c) late-juvenile BONY captured from a pond. Failure velocity is the velocity against which a fish cannot continue to swim. The investigators found that the pond-caught juveniles, and those reared in standing water without exercise conditioning, achieved average failure velocities of 74.4 and 76.0 cm/s, respectively. The exercise-conditioned juveniles, in turn, achieved an average failure velocity of 87.4 cm/s. BONY performance in the experiment was stronger than that of flannelmouth sucker, RASU, and spikedace (*Meda fulgida*).

- Mueller et al. (2007) found that late-juvenile BONY (not conditioned by prior exercise) achieved an average swimming failure velocity of 59.98 cm/s (temperature not specified). The authors noted that this result should be highly conservative, as the BONY in the experiment were not tested against velocities greater than 4.5 body lengths per second (approximately 80 cm/s). Juvenile BONY exercised for comparison unfortunately died during the experiment, preventing comparison. Juvenile BONY endurance again substantially exceeded that of RASU.

Flow and turbulence at all scales along the LCR depend on the design and operation of the water storage-delivery system, and pond design and operations, which together includes all dam and pond operations. Within individual macrohabitats, flow and turbulence also depend on tributary inflow and on channel, reservoir, and pond geometry. Flow 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 moderately large (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]). Weather—a factor outside the scope of this CEM—also affects flow/turbulence through the effects of storms on tributary inflows and wave formation. Ongoing research may address the topic of flow velocity/turbulence associations for BONY through LCR MSCP Work Tasks C25, Imperial Ponds Native Fish Research; C39, Post-Stocking Distribution and Survival of Bonytail in Reach 3; C41, Role of Artificial Habitat in Survival of Razorback Sucker and Bonytail; C49, Investigations of Razorback Sucker and Bonytail Movements and Habitat Use Downstream from Parker Dam; C58, Investigating Shoreline Habitat Cover for Bonytail; and C64, Post-Stocking Movement, Distribution, and Habitat Use of Razorback Sucker and Bonytail (Reclamation 2014).

WATER TEMPERATURE

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

Water temperature may affect BONY directly by affecting the timing of spawning, embryo development, growth and development following hatching, and metabolic rates and activity levels (e.g., swimming performance):

- BONY spawning coincides roughly with the arrival of water temperatures in the range of 18–21°C (Minckley 1991; Mueller 2006). As noted above (see chapter 2), the change in water temperature appears to be a stronger, more consistent spawning cue than any change in river discharge.

- BONY eggs exhibit maximum hatching rates in water in the range of 18–21 °C (Hamman 1982, 1985; Marsh 1985; Mueller 2006; Kappenman et al. 2012). BONY eggs die or achieve very low (e.g., 5 percent or lower) hatching rates when incubated at temperatures below 14 °C or above 26 °C, versus 50–70 percent at 14 °C, 40–100 percent at 20 °C, and

70–90 percent at 26 °C (Bulkley et al. 1982; Hamman 1982; Marsh 1985). However, Bulkley et al. (1982) also found that BONY eggs were more susceptible to fungal infection when incubated at 26 °C.

- BONY egg incubation times vary with temperature, from an average of 10 days at 14 °C, to 4–7 days at 20–21 °C, to only 3 days at 26 °C with an incubation time of 3 days (Bulkley et al. 1982; Hamman 1982). Marsh (1985) also reported that BONY larvae at swim-up are larger (8.6 mm) at 20 °C versus that at 15 or 26°C.

- Hatchery-reared juvenile BONY tested in a laboratory setting achieved their greatest weight gain during development at 25.9 °C and their lowest at 14.2 °C, among the temperatures tested by Kappenman et al. (2012). The investigators found that "Temperatures < 14 °C depressed growth, 14–20 °C provided incremental growth, and 22–26 °C allowed accelerated growth." BONY rearing facilities report greatest rates of growth at temperatures between 16.3 and 24 °C, but feeding practices and other factors may contribute to this wider range of variation (Sykes 2011). Wydoski (1994, cited in Pacey and Marsh 2008a) found that BONY growth ceases at temperatures ≤ 10 °C.

- Juvenile and adult BONY have greater swimming strength and endurance in water above 20 °C (see "Water Flow/Turbulence," this chapter). Gorman and VanHoosen (2000) also found that BONY juveniles from rearing ponds were lethargic in cold (12 °C) water, but more active at 18 °C, and fully active throughout the water column at 24 °C. These results at colder temperatures mirror those of Escandon (1994, cited in Pacey and Marsh 2008a), who recorded very low BONY metabolic rates at 15 °C. BONY avoid cold tailwaters created by hypolimnetic discharges from reservoirs (Minckley 1991; Clarkson and Childs 2000; Bestgen et al. 2008). In fact, Bulkley et al. (1982) found that, given a choice of water temperatures in which to position themselves in laboratory experiments, BONY preferred to locate themselves in water at 24.2 °C. However, this preferendum varied among BONY first acclimated to different starting temperatures: BONY acclimated at 14 °C showed an average preference for water at 17.9 °C, a preference for water at 22.5 °C after acclimation at 20 °C, and a preference for water at 25.1 °C after acclimation at 26 °C.

- BONY can tolerate fairly high water temperatures if allowed to acclimate: up to 37 °C after acclimation at 25 °C and up to 39 °C after acclimation at 30 °C (Carveth et al. 2006).

- Finally, Pacey and Marsh (2008a) suggested from hatchery data that BONY growing to sexual maturity in colder waters may be more likely to mature as females than as males.

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

- BONY experience higher levels of stress from several forms of handling when handled at higher temperatures (Montony 2008; Portz 2009; Sykes 2011; Hunt et al. 2012).

- Colder water temperatures along the Colorado River and its tributaries (e.g., associated with winter and early spring, higher-elevation headwaters, or hypolimnetic discharges from dams) are known or proposed to support lower rates of primary productivity, and lower densities and different taxonomic mixes of benthic invertebrates, thus potentially affecting the BONY diet (Carothers and Minckley 1981; Angradi 1994; Stevens et al. 1997; Benenati et al. 2000; Hoffnagle 2001; Bestgen et al. 2006; Wellard Kelly et al. 2013).

- Warmer water temperatures may support higher abundances, activity levels, or reproductive activity among several non-native micro- and macroinvertebrates known to occur in the Colorado River basin, the activities of which could affect BONY (see “Infectious Agents” and “Invertebrates and Particulate Organic Matter,” this chapter). These non-native species include virile crayfish (Martinez 2012), quagga mussel (Nalepa 2010), golden alga (Baker et al. 2009; Brooks et al. 2011), and various parasites (Carothers et al. 1981; Brouder and Hoffnagle 1997; Lenon et al. 2002; Bestgen et al. 2006; Hansen et al. 2006; Archdeacon et al. 2010; Linder et al. 2012).

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

- Water temperatures are known or suspected to affect the activity of cold-intolerant non-native fishes that may or could prey on or compete with BONY (Marsh and Pacey 2005; Bestgen et al. 2008; Yard et al. 2011). For example, cold hypolimnetic releases from dams may force these non-native species to shift further downstream year round (e.g., smallmouth bass) or at least seasonally (e.g., channel catfish), but periods of warmer water during droughts may allow these non-natives back into these same waters (Joseph et al. 1977; Valdez et al. 1990; Hoffnagle 2001; Anderson and Stewart 2007; Bestgen et al. 2007a, 2007b). In turn, Martinez (2012) noted that climate change may favor expansion of cold-water intolerant species such as smallmouth bass, a likely predator of BONY (see “Aquatic Vertebrates,” this chapter).

Water temperatures along the river and its lakes depend strongly on operational decisions at the dams along the LCR main stem, which affect the temperatures of dam releases and also affect water depths (Clarkson and Childs 2000; Reclamation 2004; Bestgen et al. 2008), which, in turn, affect thermal gradients in the reservoirs. Similarly, groundwater pumped into refuge ponds can alter water temperatures within these isolated waters. Ongoing research addresses the topic of water temperature associations for BONY through LCR MSCP Work Tasks C25, Imperial Ponds Native Fish Research; C32, Determination of Salinity, Temperature, pH, and Oxygen Limits for Bonytail and Razorback Sucker; C39, Post-Stocking Distribution and Survival of Bonytail in Reach 3; and C49, Investigations of Razorback Sucker and Bonytail Movements and Habitat Use Downstream from Parker Dam (Reclamation 2014).

Chapter 5 – Controlling Factors

Controlling factors consist of environmental conditions and dynamics, both natural and anthropogenic, which significantly affect the abundance, spatial and temporal distributions, and quality of habitat elements. They may also significantly directly affect some critical biological activities or processes. A hierarchy of such factors exists, with long-term dynamics of climate and geology at the top. However, this CEM focuses on eight immediate controlling factors that lie within the scope of potential human manipulation. The eight 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 6 lists the eight controlling factors and the habitat elements they *directly* affect.

Table 6.—Habitat elements directly affected by controlling factors

Controlling factor ➔ **➔ Habitat element**	Augmentation program operations	Channel, lake, and pond design and operations	Fishing activity and fisheries management	Motorboat activity	Nuisance species introduction and management	Tributary inflows	Wastewater and other contaminant inflows	Water storage-delivery system design and operations
Aquatic macrophytes					X			
Aquatic vertebrates			X		X			
Birds and mammals								
Fishing encounters			X					
Infectious agents	X		X		X		X	
Invertebrates and particulate organic matter					X	X	X	
Macrohabitat geometry		X				X		X
Mesohabitat geometry/cover		X				X		
Post-rearing transport and release methods	X							
Pre-release conditioning	X							
Scientific study	X							
Substrate texture/dynamics				X		X		X
Turbidity		X				X	X	X
Water chemistry						X	X	X
Water depth		X						X
Water flow/turbulence				X		X	X	X
Water temperature						X	X	X

AUGMENTATION PROGRAM OPERATIONS

This factor addresses the activities of Reclamation, the USFWS, and the States and Tribes in managing the joint BONY augmentation program (Reclamation 2006). The program covers all efforts to maintain the health, genetic diversity, and fertility of BONY broodstock; condition cohorts to ranges of flow and temperature conditions and predator interactions they will likely encounter after release; and assemble and release size-appropriate cohorts into LCR Reaches 3–5, including ponds in created backwater habitat.

CHANNEL, LAKE, AND POND DESIGN AND OPERATIONS

This factor addresses the activities of Reclamation, the USFWS, and the States and Tribes in managing the geometry of the river channel, river impoundments, off-channel habitats, and isolated ponds. It covers both historic and ongoing 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 (Beland 1953; Ohmart et al. 1988; Mueller and Marsh 2002; Reclamation 2004). These activities strongly shape macro- and mesohabitat geometry and moderately shape depth profiles throughout the system, particularly in ponds. However, areas of active mechanical shaping along the channel and refuge ponds are spatially limited and only moderately frequent (LCR MSCP biologists 2013, personal communications). Channel, shoreline, and pond management activities, such as dredging and bank maintenance, can disturb sediment in ways that also may produce localized turbidity that disperses with distance from the activity. The Habitat Conservation Plan specifically recognizes this as one of the ways in which Federal actions may routinely affect BONY (Reclamation 2004). However, the effects will be localized and brief due to the limited flow velocities present in the regulated LCR.

FISHING ACTIVITY AND FISHERIES MANAGEMENT

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

Management of sport fisheries includes regulating fishing activities, and introducing and/or stocking sport species, as well as bait and forage species for the sport fisheries. These management activities and the legacies of past such activities may affect the LCR ecosystem in several ways, including introducing infectious agents, shaping public perceptions of the relative value of sport fisheries versus native species recovery programs, shaping the spectrum of species that prey on or compete with BONY, and altering physical habitat. The potential for conflicts between sport fishery management and the conservation of native fishes along the Colorado River is a longstanding concern (Holden 1991; Minckley 1991; NRC 1991; Rolston 1991; Mueller and Marsh 2002; Minckley et al. 2003; Marsh and Pacey 2005; Clarkson et al. 2005). Table 5, chapter 4, lists non-native sport species introduced into the LCR, and species introduced as bait or forage for the sport fisheries, and indicates whether they are known to prey on or compete with BONY or if they could be proposed as competitors based on their feeding ecology. Infectious (including parasitic) organisms that are known to infect BONY and likely introduced with non-native sport fishes include *Lerneae* spp. and *Myxobolus* spp. (Flagg 1982) (see "Infectious Agents," chapter 4).

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

Recreational fishers also have effects on BONY. As noted earlier, BONY can be taken readily with a baited hook, and recreational anglers occasionally catch them along the LCR main stem and in its reservoirs (Minckley 1991; USFWS 1990, 2002a; Mueller 2006; Minckley and Thorson 2007; Karam and Marsh 2010; Karam et al. 2011, 2012, 2013; Wolff et al. 2012). Signs advise anglers to release any BONY caught; however, as noted above, BONY released after capture are susceptible to capture myopathy, leading to death. Anglers also are known to transplant desired sport fishes to water bodies where they appear to be absent (Wolff et al. 2012). Mueller (2006) hypothesized that this was the source of the largemouth bass introduced into Cibola High Levee Pond in 2004, which spawned a large cohort that devastated the pond's BONY and RASU populations, ending a 5-year study of their ecology.

MOTORBOAT ACTIVITY

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

NUISANCE SPECIES INTRODUCTION AND MANAGEMENT

This factor addresses animals and plants introduced into LCR waters and wetlands *but not officially managed by the States for recreation or as bait or forage for a sport fishery* that affect BONY survival or reproduction. The introductions may have occurred intentionally 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 BONY during one or more life stages; cause other alterations to the aquatic food web that affect BONY; alter water chemistry; or affect physical habitat features such as cover, substrate stability, or turbidity. As noted above (see "Aquatic Macrophytes," "Aquatic Vertebrates," and "Invertebrates and Particulate Organic Matter," chapter 4), introduced nuisance species along the LCR include plants, amphibians, crustaceans, and fishes. Interactions with BONY include the following:

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

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

- Asian clam, quagga mussel, and zebra mussel can blanket benthic habitat and filter out large quantities of plankton, increasing water clarity, potentially allowing more growth of emergent macrophytes across a given shallow-water setting, as suggested by LCR MSCP biologists 2013, (personal communications).

- Bullfrog larvae prey on small fishes but also may be prey for adult BONY. Rogalski and Skelly (2012) also reported a possible positive relationship between common reed expansion and non-native American bullfrog productivity.

- Northern crayfish and red swamp crayfish prey on small BONY (larvae and fry) (Horn et al. 1994; Mueller 2006; Mueller et al. 2006) and also compete with them for food (particulate organic matter and smaller aquatic invertebrates). However, adult BONY also feed on crayfish in turn, reducing the impacts as predators and competitors (Lenon et al. 2002; Mueller 2006; Marsh et al. 2013b).

- Introduced threadfin shad (*Dorosoma petenense*), red shiner (*Notropis lutrensis*), western mosquitofish (*Gambusia affinis*), and fathead minnow (*Pimephales promelas*) likely prey on and/or compete with BONY (see table 5, chapter 4).

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

TRIBUTARY INFLOWS

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

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 particulate organic matter and aquatic macrophytes (Karam et al. 2011, 2012, 2013). For these reasons, BONY 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 INFLOWS

This factor addresses the management of regulated discharges, irrigation practices, and management of contaminated sites across the watershed as well as the chemical contributions these sources make to river chemistry. The LCR receives inputs directly from 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 Laughlin, Nevada, Lake Havasu City, Arizona, and Needles, California. 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, 2010, 2011b, 2011c; Hamilton et al. 2005a, 2005b; Sanchez et al. 2005; Acharya and Adhikari 2010a, 2010b; Adhikari et al. 2011; Turner et al. 2011; Stolberg 2009, 2012).

Wastewater point-source inflow confluences also constitute distinct zones of flow variation, turbidity, water temperature, and geomorphology, constituting macrohabitats with distinct assemblages of mesohabitat types. They may also include suspended particulate organic matter. For these reasons, BONY may interact with or use wastewater confluences as distinct habitat settings as well.

Theoretically, municipal and rural wastewater could also contain pathogens that affect BONY, although no studies have been conducted to specifically investigate 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 of 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 BONY.

WATER STORAGE-DELIVERY SYSTEM DESIGN AND OPERATIONS

The LCR main stem consists of a chain of reservoirs separated by flowing reaches. The water moving through this system is highly regulated for storage and delivery (diversion) to numerous international, Federal, State, Tribal, 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 and the infrastructure built for that management together comprise almost the only factor affecting hydraulic and hydrogeomorphic dynamics along the LCR (Reclamation 2004). Water management along the system balances demand against the amount of water that enters the system from the upper basin.

This CEM also encompasses the other protected areas along the LCR managed as BONY habitat under the auspices of the LCR MSCP Habitat Conservation Plan. Water depths and flows in these areas depend on the regulated conditions along the river and 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 operators often release water from a single thermal layer in each reservoir, either the epilimnion or the hypolimnion, each of which has a unique chemistry and thermal range. These releases, in turn, affect 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 five sections, each presenting the CEM for a single BONY life stage. For each life stage, the text and diagrams identify its life-stage outcomes; its critical biological activities and processes; the habitat elements that support or limit the success of its critical biological activities and processes; the controlling factors that determine the abundance, distribution, and other important qualities of these habitat elements; and the causal links among them. The model sections specifically refer to the river and the lakes of the LCR and other protected areas managed as BONY habitat. It does not include facilities managed exclusively for rearing BONY larvae into adults large enough for release, but it does include protected areas into which the hatchery-reared BONY are released as part of the augmentation program (Reclamation 2006). The model addresses the LCR 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 1 for further details):

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

- **Magnitude** refers to "… the degree to which a linkage controls the outcome *relative to other drivers*" (DiGennaro et al. 2012). Magnitude takes into account the spatial and temporal scale of the causal relationship as well as the strength (intensity) of the relationship at any single place and time. The present methodology separately rates the intensity, spatial scale, and temporal scale of each link on a three-part scale from "Low" to

"High" and assesses overall link magnitude by averaging the ratings for these three. If it is not possible to estimate the intensity, spatial scale, or temporal scale of a link, the subattribute is rated as "Unknown" and ignored in the averaging. If all three subattributes are "Unknown," however, the overall link magnitude is rated as "Unknown." Just as the terms for link character provide information analogous to the sign of a correlation coefficient, the terms for link magnitude provide information analogous to the size of a correlation coefficient.

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

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

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

A separate spreadsheet is used to record the assessment of the character and direction, magnitude, predictability, and scientific understanding for each causal link along with the underlying rationale and citations for each life stage. The CEM for each life stage, as cataloged in its spreadsheet, is illustrated with diagrams showing the controlling factors, habitat elements, critical biological activities and processes, and causal links identified for that life stage. A diagram may also visually display information on the character and direction, magnitude, predictability, and/or scientific understanding of every link. The diagrams use a common set of conventions for identifying the controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes as well as for displaying information about the causal links. Figure 2 illustrates these conventions.

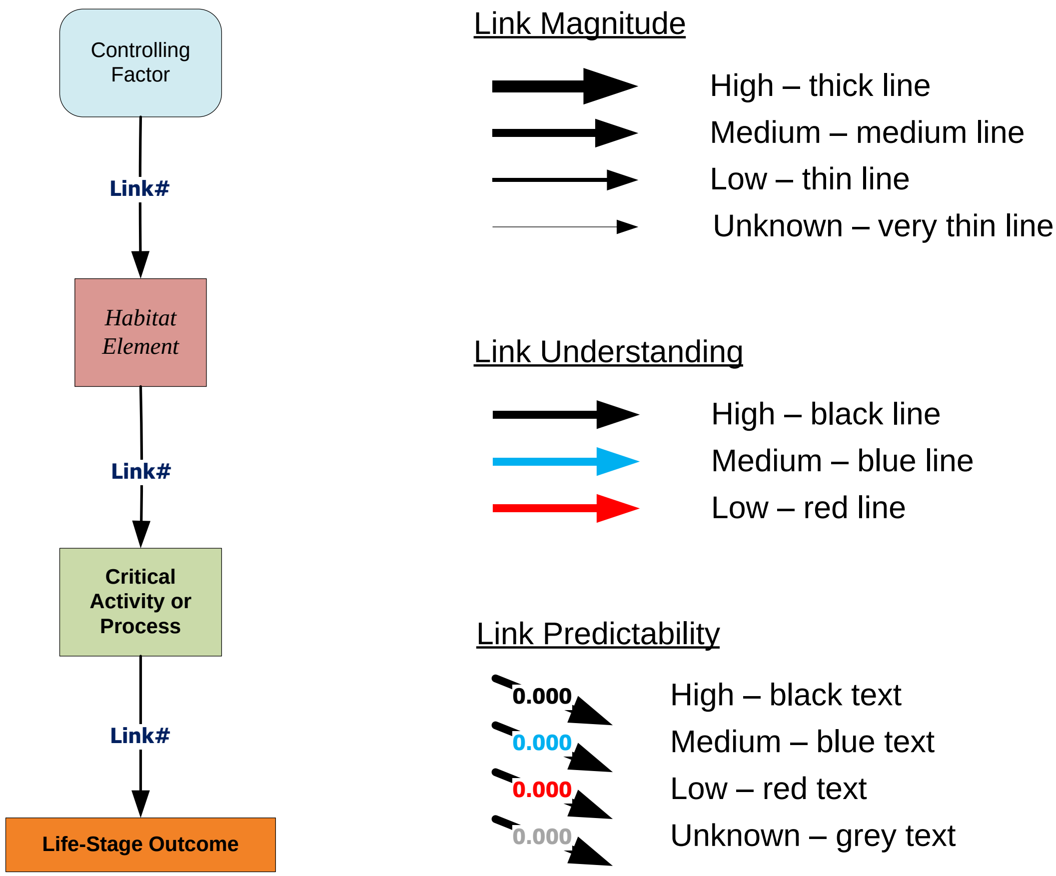


Figure 2.—Diagram conventions for LCR MSCP CEMs.

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 five BONY life stages. For this reason, the discussion of controlling factor-habitat element linkages across all five life stages appears in a subsequent chapter.

BONY LIFE STAGE 1 – EGGS AND EARLY LARVAE

As described in chapter 2, this life stage begins with the end of involvement of the spawning adults in the fate of the eggs, when the spawning individuals depart the scene of each individual spawning event. The life stage continues through egg hardening and adhesion, incubation, and hatching and ends with larval swim-up at approximately 15 mm TL. The life stage has a single life-stage outcome, designated S_{EL}, the rate of survival of (recruitment from) the life stage (see figure 1).

The CEM, shown in figure 3, identifies 6 (of 11) critical biological activities or processes affecting the single outcome for this life stage, presented here in alphabetical order:

1. *Chemical stress*: The CEM recognizes this relationship as a theoretical possibility only. The literature presents no evidence that BONY eggs and early larvae outside of hatcheries experience levels of chemical stress sufficient to affect their survivorship, but few close observations exist for egg and larval development outside of hatcheries (Mueller 2006). The CEM recognizes this relationship only because the possible detrimental effects of pollution on BONY in general was a historic concern in the literature (e.g., USFWS 2002a; Minckley et al. 2003). However, studies of the LCR have not supported this larger concern. The causal relationship therefore warrants a low rating for magnitude but also a low rating for understanding given the rarity of observations of this life stage outside of hatcheries.

2. *Disease*: The literature includes only one report of infections in BONY eggs outside of a hatchery (Mueller 2006) but several reports from inside hatcheries (reviewed by Pacey and Marsh 2008a; Portz 2009). However, the relationship between egg or larval disease and mortality in hatcheries does not provide an indicator of the strength that this relationship would have outside of hatcheries. Water conditions and exposures to infectious agents are too different between the two settings. The observations of "wild" eggs and larvae by Mueller (2006) at Cibola High Levee Pond suggested that only a few eggs became infected, in this case by fungi. The causal relationship therefore again warrants a low rating for magnitude but also a low rating for understanding given the rarity of observations of this life stage outside of hatcheries.

3. *Egg settling and adhesion*: Successful completion of this life stage outside of hatcheries requires that BONY eggs first must settle onto and adhere to the substrate at the spawning site, escaping predation and escaping being swept away into environments inhospitable to egg

maturation. Mueller (2006) described predatory attacks on freshly released BONY eggs (see below) both in the water column and in the substrate into which eggs may have already settled. In addition to the resulting mortality due to predation (see below), these attacks disrupt the process of egg settling and adhesion. Other disturbances to water currents or substrates at spawning sites similarly can disrupt the process of egg settling and adhesion. Observations at hatcheries, in turn, confirm that disruptions to egg settling and adhesion reduce survivorship (see reviews by Pacey and Marsh 2008a; Portz 2009). The causal relationship therefore warrants a high rating for magnitude and also for understanding. Understanding of the relationship rests on strong ecological principles and observations in hatcheries and isolated ponds.

4. *Mechanical stress*: The literature presents no evidence that BONY eggs and early larvae outside of hatcheries experience levels of mechanical stress sufficient to affect their survivorship *independent* of factors that may disrupt egg settling and adhesion. Few close observations exist for egg and larval development outside of hatcheries (e.g., Mueller 2006), but observations at hatcheries indicate that neither BONY eggs (once they hardened) nor BONY larvae are easily injured by handling (Hamman 1982, 1985; Pacey and Marsh 2008a; Portz 2009). The CEM recognizes this relationship only because it is a theoretical possibility that should be considered. Further, among five habitat elements potentially capable of causing mechanical stress on BONY eggs or early larvae, all warrant ratings of low for magnitude: scientific handling, substrate texture/ dynamics, water depth, water flow/turbulence, and predation, as explained below. The causal relationship therefore warrants a low rating for magnitude but a medium rating for understanding given the number of observations from hatcheries and field settings indicating that mechanical stress does not significantly contribute to mortality at this life stage independent of factors that may disrupt egg settling and adhesion.

5. *Predation*: This is the most commonly proposed cause of poor survivorship among BONY eggs and early larvae outside of hatcheries (Mueller 2006). Aquatic invertebrates, fish, birds, and mammals that are capable of, known, or suspected to prey on BONY eggs and early larvae are present throughout the LCR year round (see chapter 3). Further, efforts to keep predatory fishes out of isolated ponds have not always succeeded (Mueller 2006). Indeed, known predators on BONY eggs and larvae include adult BONY and RASU (see above). However, there are insufficient data to confirm that the very low survivorship of BONY eggs and early larvae outside of hatcheries is mostly due to predation. Direct observations of predation on BONY eggs or larvae are limited to Cibola High Levee Pond (Mueller 2006). Inferences concerning this causal relationship mostly rest on studies of RASU and on comparisons of survivorship among BONY eggs and larvae in predator-dense versus

predator-free ponds (Mueller 2006). The causal relationship therefore warrants a high rating for magnitude but a low rating for understanding.

6. *Thermal stress*: The literature does not suggest that BONY eggs or early larvae outside of hatcheries experience levels of thermal stress sufficient to affect their survivorship. However, thermally stressful conditions may simply be rare in the present-day system, especially in isolated ponds with highly regulated water conditions. BONY eggs and larvae in hatcheries also appear to be relatively insensitive to variation in water temperature, within fairly broad ranges of tolerance (see chapter 4; Pacey and Marsh 2008a; Portz 2009). The causal relationship warrants a low rating for magnitude but also a low rating for understanding given the rarity of observations of this life stage outside of hatcheries.

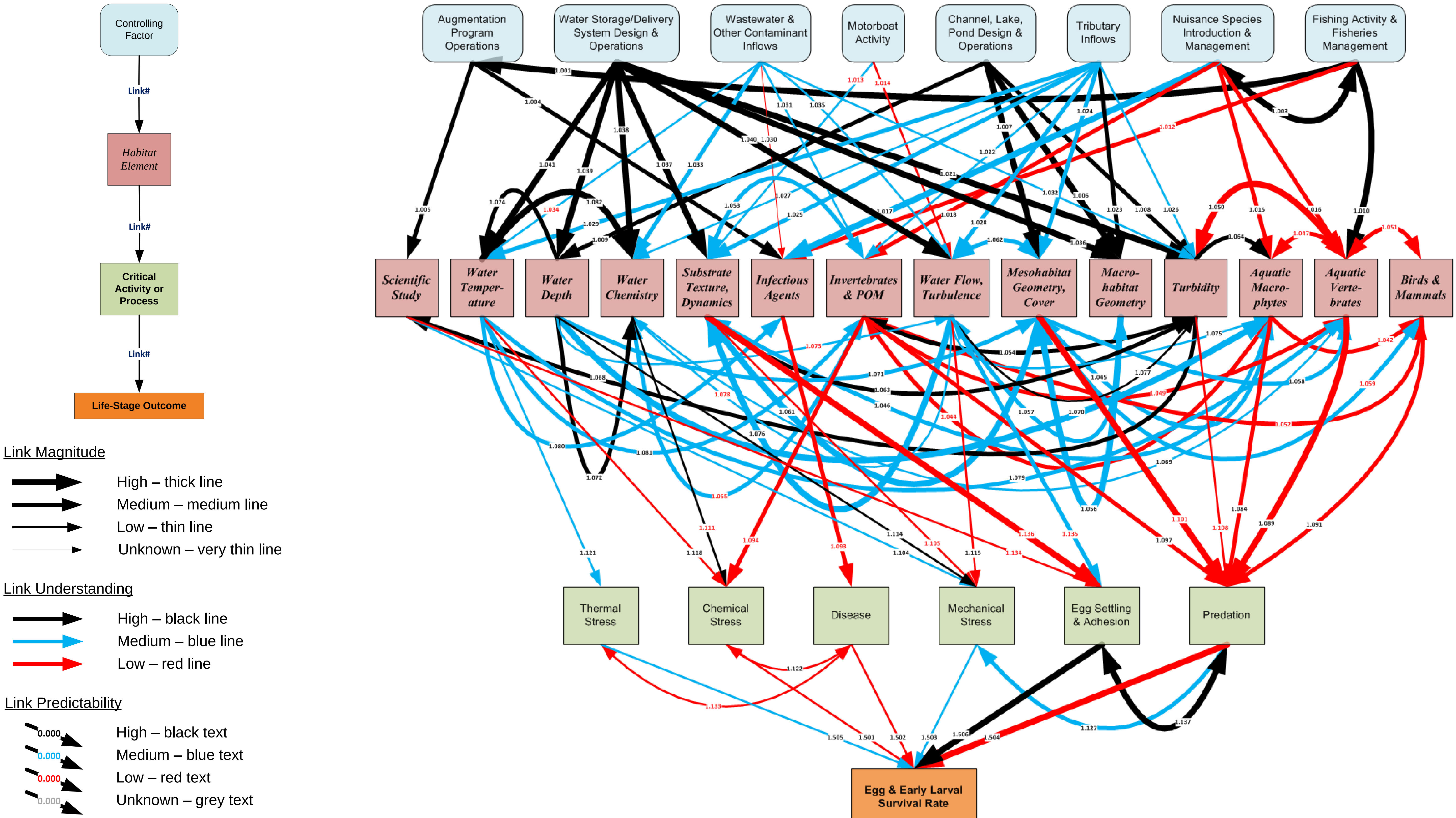


Figure 3.—BONY life stage 1 – eggs and early larvae.

BONY LIFE STAGE 2 – FRY AND JUVENILES

As described in chapter 2, this life stage covers the time from larval swim-up and dispersal to sexual maturation, beginning at roughly 15 mm TL and extending to roughly 100–150 mm TL. Upon reaching swim-up, BONY larvae must find and settle in suitable nursery habitat. They presumably achieve this primarily through drifting because of their limited swimming abilities. Little is known about the locations or properties of BONY nursery sites prior to river regulation, how far BONY larvae may have drifted between spawning and nursery sites, or whether BONY larvae or juvenile in natural settings remain at just one nursery site or move among several sites as they mature (Mueller 2006). This life stage has a single life-stage outcome, designated S_{FJ}, the rate of survival of (recruitment from) the life stage (see figure 1).

The CEM, shown in figure 4, identifies 7 (of 11) critical biological activities or processes affecting the single outcome for this life stage, presented here in alphabetical order:

1. *Chemical stress*: The CEM recognizes this relationship as a theoretical possibility only. The literature presents no evidence that BONY fry or juveniles outside of hatcheries experience levels of chemical stress sufficient to affect their survivorship, but few close observations exist for this life stage development outside of hatcheries (Mueller 2006). The CEM recognizes this relationship only because the possible detrimental effects of pollution on BONY in general was a historic concern in the literature (e.g., USFWS 2002a; Minckley et al. 2003). However, studies along the LCR have not supported this larger concern. The causal relationship therefore warrants a low rating for magnitude but also a low rating for understanding given the rarity of observations of this life stage outside of hatcheries.

2. *Disease*: The literature includes no reports of infections specifically in BONY fry or juveniles outside of hatcheries but occasional reports from inside hatcheries (reviewed by Pacey and Marsh 2008a; Portz 2009). However, the relationship between fry or juvenile disease and mortality in hatcheries does not provide an indicator of the strength that this relationship would have outside of hatcheries. Water conditions and exposures to infectious agents are too different between the two settings. The causal relationship therefore again warrants a low rating for magnitude but also a low rating for understanding given the rarity of observations of this life stage outside of hatcheries.

3. *Drifting*: BONY fry and juveniles must drift in currents to move from their natal sites to their nursery sites, or among nursery sites, because BONY spawn at sites that do not coincide with, and in fact may lie some

distance from, nursery habitat (see chapter 3 and below). However, the low currents in the present-day river, and the even lower (or non-existent) currents and close proximity of mesohabitats in isolated ponds, may provide little opportunity for such behavior (Mueller 2006). BONY fry and juveniles may try to control the timing of drift by swimming in/out of currents, as do other fishes in the LCR (Modde and Haines 2005; Valdez et al. 2011). They also may preferentially drift at night (Snyder and Meisner 1997), a behavior that may reduce predation, as has been proposed for other LCR fishes (Johnson et al. 1993; Horn et al. 1994; Johnson and Hines 1999). Drifting also may occur during only a small proportion of the time during this life stage. The causal relationship therefore warrants a medium rating for magnitude (high intensity but medium spatial scale and low temporal scale) but a low rating for understanding given the rarity of observations of this behavior or indeed observations of this life stage outside of hatcheries at all.

4. *Foraging*: Analyses of stomach contents and observations in field settings suggest that BONY fry or juveniles feed on plant litter, aquatic macrophytes, phytoplankton and zooplankton, macroinvertebrates such as smaller aquatic insect adults and larvae, smaller terrestrial insects that may fall or land on the water, and very small vertebrates such as very young bullfrog larvae and very small fish, based on studies of BONY diet and its variation with BONY size (Vanicek and Kramer 1969; Tyus et al. 1988; Lenon et al. 2002; USFWS 2002a; Marsh and Schooley 2004; Mueller 2006; Reclamation 2008; Marsh et al. 2013a). BONY fry or juveniles, by definition, must forage to survive. The causal relationship therefore warrants a high rating for magnitude. However, it warrants a low rating for understanding due to a lack of studies assessing whether low rates of foraging success among BONY fry or juveniles outside of artificial environments reduce survivorship. Studies of BONY fry or juvenile survivorship in hatcheries, in relationship to diet, provide no analogous data because hatcheries use artificial diets (Pacey and Marsh 2008a). Two studies of BONY fry or juvenile survivorship in outdoor rearing ponds, in relationship to diet, similarly provide no analogous data because of their use of artificial diets as well (Marsh and Schooley 2004; Sykes 2011).

5. *Mechanical stress*: The literature presents no evidence that BONY fry or juveniles either outside or inside hatcheries experience levels of mechanical stress sufficient to affect their survivorship. Few close observations exist for fry or juvenile development outside of hatcheries (Mueller 2006), but observations at hatcheries indicate that neither BONY fry nor juveniles are easily injured by handling (Hamman 1982, 1985; Pacey and Marsh 2008a; Portz 2009). Portz (2009), for example, described information on the impacts of handling on stress levels in juvenile BONY as “anecdotal,” and Pacey and Marsh (2008a) noted that handling reduced growth rates among “a mixture of juveniles and adults

(101–173 mm TL)" but that passive integrated transponder tagging per se did not further reduce growth. The CEM recognizes this relationship only because it is a theoretical possibility that should be considered. Further, all six habitat elements potentially capable of causing mechanical stress on BONY fry or juveniles warrant ratings of low for magnitude: fishing encounters, scientific handling, substrate texture/dynamics, water depth, and water flow/turbulence, as explained below. The causal relationship therefore warrants a low rating for magnitude but a high rating for understanding. Both hatchery and field observations indicate that mechanical stress can directly reduce survivorship at least among BONY adults, with no indications that this would be any different for BONY fry or juveniles. BONY fry or juveniles, like BONY adults, may also strongly attempt to escape capture, possibly resulting in mechanical stress (Mueller 2006).

6. *Predation*: This is the most commonly proposed cause of poor survivorship among BONY fry and juveniles outside of hatcheries (Mueller 2006) (see chapter 3). Aquatic invertebrates, fish, birds, and mammals that are capable of, known, or suspected to prey on BONY fry or juveniles are present throughout the LCR year round (see chapter 3). The aquatic predators in the system today have different gape-size limitations than the historic, native aquatic predators among which BONY evolved. Today's predators may also have different foraging behaviors than the historic predators. Together, these differences may put BONY fry and juveniles at greater risk than previously (see chapter 3). Further, efforts to keep predatory fishes out of isolated ponds have not always succeeded (Mueller 2006). However, there are insufficient data with which to confirm that the very low survivorship of BONY fry and juveniles outside of hatcheries is mostly due to predation. Direct observations of predation on BONY fry and juveniles are limited to Cibola High Levee Pond (Mueller 2006), and inferences concerning this causal relationship mostly rest on studies of RASU and on comparisons of survivorship among BONY fry and juveniles in predator-dense versus predator-free ponds (Mueller 2006). The causal relationship therefore warrants a high rating for magnitude but a medium rating for understanding.

7. *Thermal stress*: The literature does not suggest that BONY fry or juveniles outside of hatcheries experience levels of thermal stress sufficient to affect their survivorship. However, thermally stressful conditions may simply be rare in the present-day system, especially in isolated ponds with highly regulated water conditions. BONY fry or juveniles in hatcheries also appear to be relatively insensitive to variation in water temperature, within fairly broad ranges of tolerance (see chapter 4) (Pacey and Marsh 2008a; Portz 2009). The causal relationship warrants a low rating for magnitude but a medium rating for

understanding given the rarity of observations of this life stage outside of hatcheries balanced against the rarity of situations in the LCR and its off-channel wetlands and ponds in which BONY fry or juveniles may encounter potentially thermally stressful conditions.

Several critical biological activities or processes also affect the outcome of this life stage indirectly through their effects on the seven critical biological activities or processes with direct impacts listed above (figure 4). Most notably:

- Competition for food items and habitat (e.g., cover) among BONY fry and juveniles and between BONY fry or juveniles and other species may affect foraging success and predator avoidance for this life stage.

- Foraging success provides BONY fry and juveniles with the energy to enable them to swim more effectively.

- Predation on dispersing larvae could favor the survival of those with the shortest dispersal routes, particularly routes with good cover, or strongest swimming abilities (Mueller 2006; Kesner et al. 2010a, 2010b). These suggestions rest on observations of isolated ponds in which BONY have voluntarily spawned and subsequently persisted, where suspected nursery habitat lay close to known or suspected spawning areas with little or no intervening "dispersal" habitat (Mueller 2006; Kesner et al. 2010a, 2010b).

- Unsuccessful predatory attacks may also cause mechanical stress (wounding) among BONY fry and juveniles.

- Increasing swimming abilities and stamina during this life stage should enable BONY fry and juveniles to increasingly avoid or move away from potentially hazardous conditions of all kinds, forage more effectively, and navigate among mesohabitats. For example, as noted in chapter 2, as BONY mature from fry to juvenile to adult, they exhibit an expanding range of defensive and avoidance behaviors in response to predator activity, including hiding in geomorphic and vegetative cover (Mueller 2006; Marsh et al. 2013b). Covers used (see "Resting," chapter 3) include dark interstices among cobbles and boulders, entrances to beaver dams, bedrock crevices and overhangs, dense emergent and overhanging vegetation, and floating vegetation mats. Defensive behaviors include schooling and "scrumming" (Mueller 2006). In fact, schooling not associated with spawning first appears among fry and juveniles and has been reported for all subsequent age classes in both hatchery settings and ponds (Hamman 1982; Mueller et al. 2003, 2004; Mueller 2006). Fry and juveniles may form schools of as many as several hundred individuals in the daytime (Moffett 1943 cited in Mueller 2006; Jonez and Sumner 1954; Mueller 2006).

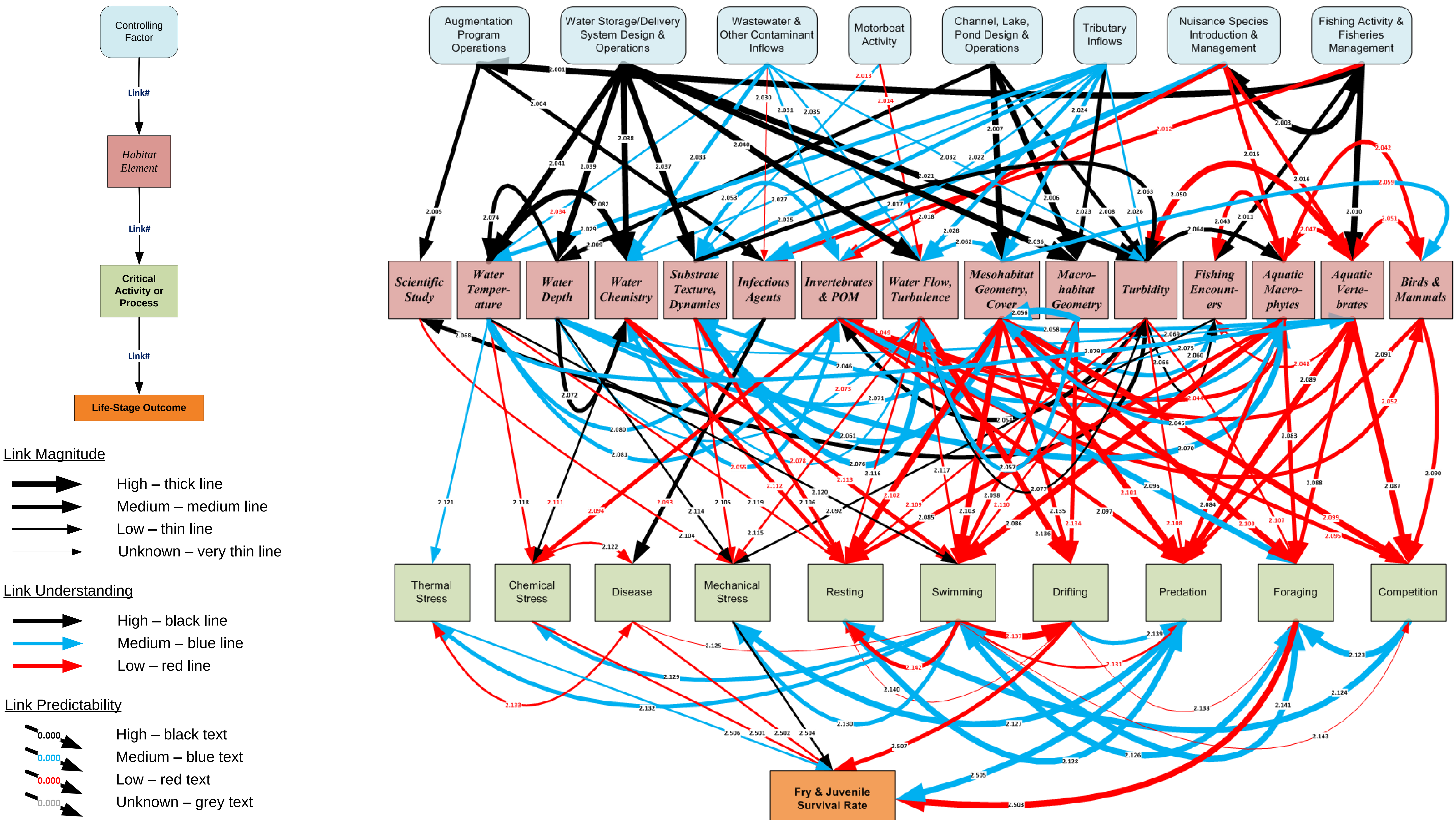


Figure 4.—BONY life stage 2 – fry and juveniles.

BONY LIFE STAGE 3 – NEWLY STOCKED ADULTS

As described in chapter 2, this life stage covers adults newly released from hatcheries during their initial acclimation to river, reservoir, or grow-out pond conditions. Stocking from hatchery broodstock is the overwhelming source of adults in open environments today; contributions from wild-reproducing BONY are thought to be minimal. Under the augmentation program, BONY were originally released from hatcheries as "fingerlings," approximately 100 mm TL, but shifted to releasing only adults after 1993–94 in an effort to reduce predation on the released cohorts (Minckley et al. 2003). A goal of the augmentation program today is to release BONY from hatcheries when they reach ≈ 300 mm TL (305 mm TL in California), which can occur after 8 months to 2 years, varying in part with fish density (Sykes 2011). However, hatcheries cannot easily separate BONY by size when preparing a cohort for release, and releases may include individuals as small as 250 mm TL (Pacey and Marsh 2008a; LCR MSCP biologists 2014, personal communications). Newly stocked adults may remain behaviorally distinct from wild-born (but currently rare) BONY for some time after release. The component has a separate input, S_{HR}, for the rate of stocking from hatcheries, but this input and the hatchery programs behind it are not part of the CEM. The life stage has a single life-stage outcome, designated S_{NA}, the rate of survival of the newly stocked adults to become established adults.

The CEM, shown in figure 5, identifies 6 (of 11) critical biological activities or processes affecting the single outcome for this life stage, presented here in alphabetical order:

1. *Chemical stress*: The CEM recognizes this relationship as a theoretical possibility only. The literature presents no evidence that newly stocked BONY adults experience levels of chemical stress sufficient to affect their survivorship. If *acute* chemical stress were a significant problem, for example, large numbers of freshly deceased BONY would have been observed shortly after release, but this has never been observed. The CEM recognizes this relationship only because the possible detrimental effects of pollution on BONY in general was a historic concern in the literature (e.g., USFWS 2002a; Minckley et al. 2003). However, studies along the LCR have not supported this larger concern. The causal relationship therefore warrants a low rating for magnitude but also a low rating for understanding given the absence of systematic observations concerning chemical stress following release.

2. *Disease*: The literature includes no reports of infections specifically in newly stocked BONY adults. The relationship between BONY adult disease and mortality in hatcheries (Pacey and Marsh 2008a; Portz 2009) does not provide an indicator of the strength that this relationship would

have outside of hatcheries. Water conditions and exposures to infectious agents are too different between the two settings. The causal relationship therefore again warrants a low rating for magnitude and also a low rating for understanding given the rarity of observations of this life stage outside of hatcheries.

3. *Foraging*: The literature includes no reports of foraging behavior specifically among newly stocked BONY adults. Prior to their release, reared BONY are fed artificial diets, sometimes supplemented with zooplankton that pass through the water filters at the rearing facilities (Marsh and Schooley 2004; Pacey and Marsh 2008a; Sykes 2011). They thus have no experience with the range of natural food items or prey behaviors they will encounter following release. Discussions of the need for pre-release conditioning of BONY in hatcheries (see chapter 4) sometimes note the possible importance of conditioning to this range of wild food items and prey behaviors (e.g., compare Lentsch et al. 1995; Ward and Hilwig 2004; Reclamation 2006; Mueller 2007; Mueller et al. 2007; Bestgen et al. 2008; Pacey and Marsh 2008a; Portz 2009; Ward and Figiel 2013). However, the topic has not been specifically investigated (LCR MSCP biologists 2014, personal communications). Of course, newly stocked BONY adults must forage to survive. The causal relationship therefore warrants a high rating for magnitude but warrants a low rating for understanding.

4. *Mechanical stress*: The literature presents no evidence that newly stocked BONY adults experience levels of mechanical stress sufficient to affect their survivorship. However, it is a topic of concern, specifically whether the process of handling and transport of hatchery-reared BONY for release may cause them mechanical stress that reduces their fitness upon release (see chapter 4) (Sykes 2013). Newly released BONY adults are also subject to scientific capture and handling for months following release, driven by the needs of the augmentation program to assess the fate of the fish following release (see chapter 4) (Mueller et al. 2014). BONY may be particularly vulnerable to stress during capture and handling (Tyus et al. 1999; Paukert et al. 2005; Mueller 2006). The CEM recognizes this relationship only because it is a theoretical possibility that should be considered. The model identifies six habitat elements as potentially capable of causing mechanical stress on newly stocked BONY adults. Four of these warrant ratings of low for magnitude: post-rearing transport and release, substrate texture/dynamics, water depth, and water flow/turbulence. Scientific study and fishing encounters, in turn, warrant ratings of medium for magnitude for the risks of injury they pose for newly stocked BONY adults. The causal relationship therefore warrants a low rating for magnitude but a high rating for understanding. Both

hatchery and field observations indicate that mechanical stress can directly reduce survivorship at least among BONY adults, with no indications that this would be any different for newly stocked BONY.

5. *Predation*: This is the most commonly proposed cause of the observed poor survivorship among newly stocked BONY adults (Bozek et al. 1984; USFWS 1990, 2002a; Minckley 1991; Lentsch et al. 1995; Minckley et al. 2003; Christopherson et al. 2004; Ward and Hilwig 2004; Brunson and Christopherson 2005; Marsh and Pacey 2005; Modde and Haines 2005; Mueller et al. 2006, 2007; Mueller 2005, 2006, 2007; Reclamation 2006, 2008; Bestgen et al. 2008; Kesner et al. 2008, 2010a, 2010b; Pacey and Marsh 2008b; Portz 2009; Karam and Marsh 2010; Karam et al. 2013; Ward and Figiel 2013; Mueller et al. 2014). Aquatic, avian, and terrestrial fauna able or known to prey on BONY are abundant, widespread, and active year round, and they include non-native aquatic predators with different gape-size limitations and/or different predatory behaviors than those present among the native aquatic predators among which BONY evolved. The primary role of predation in the high rate of mortality among newly stocked BONY adults remains difficult to directly test. However, probative studies include observations of BONY remains in stomach contents of predators (Bestgen et al. 2008; Karam and Marsh 2010) and the effects of introductions of specific predators into isolated ponds previously free of these predators (Christopherson et al. 2004; Mueller 2005, 2006). The causal relationship warrants a high rating for magnitude and a medium rating for understanding.

6. *Thermal stress*: The literature does not suggest that newly stocked BONY adults experience levels of thermal stress sufficient to affect their survivorship. However, thermally stressful conditions may simply be rare in the present-day system, especially in isolated ponds with highly regulated water conditions. Further, BONY adults in hatcheries appear relatively insensitive to variation in water temperature, within fairly broad ranges of tolerance (see chapter 4) (Pacey and Marsh 2008a; Portz 2009). Consequently, the causal relationship warrants a low rating for magnitude and a medium rating for understanding.

Several critical biological activities or processes also affect the outcome of this life stage indirectly through their effects on the six biological activities or processes with direct impacts listed above (figure 5). Most notably:

- Competition for food items and habitat (e.g., cover) among newly stocked BONY adults and between them and other species may affect foraging success and predator avoidance for this life stage.

- Foraging success provides newly stocked BONY adults with the energy to enable them to swim more effectively.

- Unsuccessful predatory attacks may also cause mechanical stress (wounding) among newly stocked BONY adults.

- Swimming abilities among newly stocked BONY adults affect their capacities to avoid or move away from potentially hazardous conditions of all kinds, forage effectively, and navigate among mesohabitats. However, the extent to which newly stocked BONY adults exhibit the range of defensive and avoidance behaviors observed among BONY with more experience outside of hatcheries is not known (see "Pre-Release Conditioning," chapter 4).

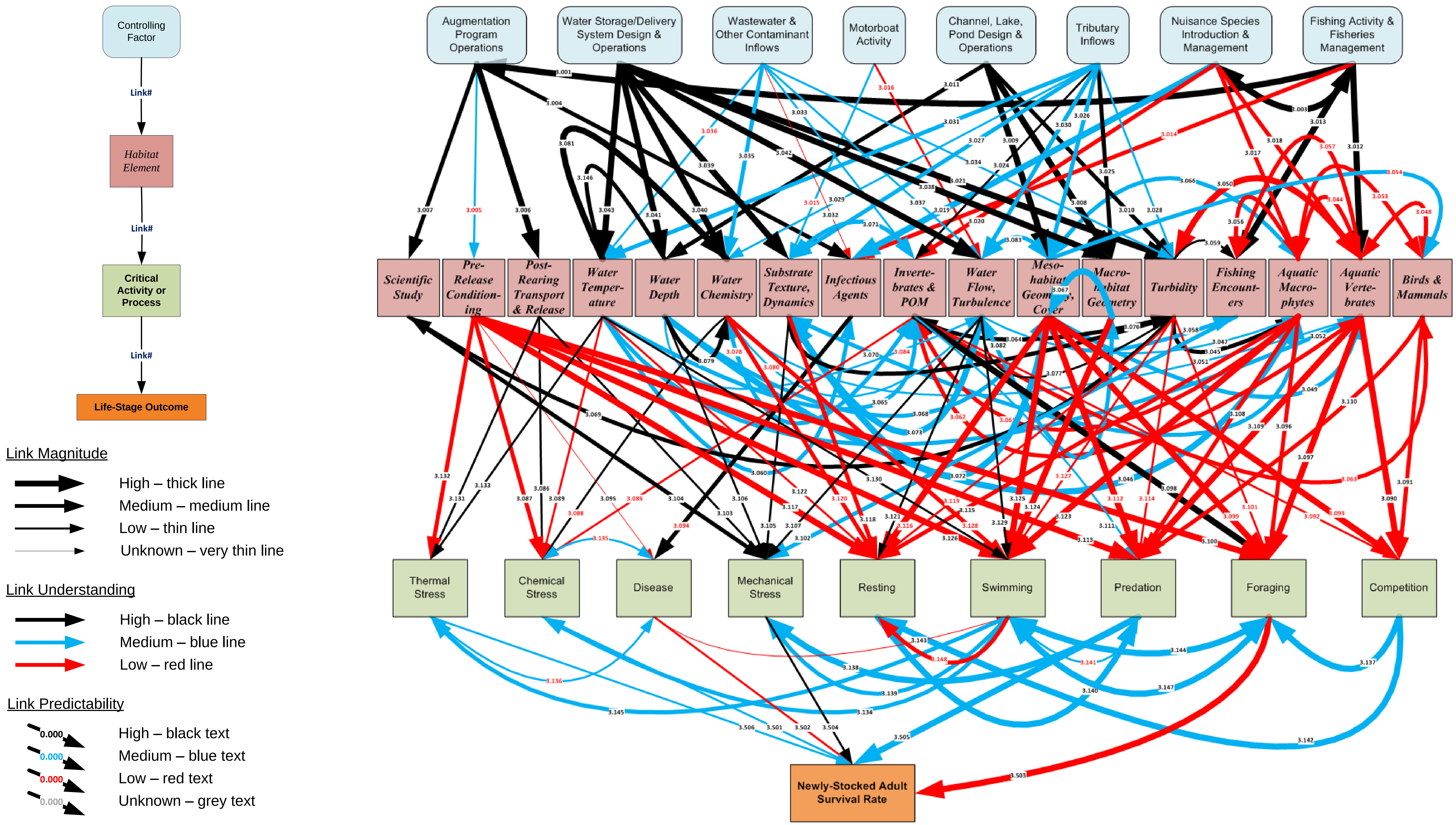


Figure 5.—BONY life stage 3 – newly stocked adults.

BONY LIFE STAGE 4 – ESTABLISHED ADULTS

As described in chapter 2, this life stage covers the entire lifespan for adult BONY established in open habitats, including grow-out ponds, but not hatcheries. The life stage begins when BONY fully achieve sexual maturity, with body sizes in the range of 100–150 mm TL (Mueller 2006, 2007; Pacey and Marsh 2008a), roughly 4–6 months after hatching, Age–0. Adults historically achieved lengths > 500 mm TL but usually less; today, individuals > 400 mm are rare, and most achieve lengths in the range of 300–400 mm TL (Minckley 1991; USFWS 2002a; Mueller 2006; Pacey and Marsh 2008a; Reclamation 2008). The life stage has two life-stage outcomes: (a) S_{EA}, the rate of survival of established adults from year to year so that they remain part of the adult population, and (b) P_{SP}, the rate of reproductive participation – the percentage of adults that participate in and contribute gametes to spawning per year.

The CEM, shown in figure 6, identifies 6 (of 11) critical biological activities or processes affecting the two outcomes for this life stage, presented here in alphabetical order:

1. *Chemical stress*: The CEM recognizes this relationship as a theoretical possibility affecting both life-stage outcomes. The literature presents no evidence established BONY adults experience levels of chemical stress sufficient to affect their survivorship or reproductive participation. The CEM recognizes this relationship only because the possible detrimental effects of pollution on BONY in general was a historic concern in the literature (e.g., USFWS 2002a; Minckley et al. 2003). However, studies of the LCR have not supported this larger concern. The causal relationship for both life-stage outcomes therefore warrants a low rating for magnitude but also a low rating for understanding given the absence of systematic observations concerning chemical stress following release.

2. *Disease*: The literature includes no reports of infections specifically in established BONY adults sufficient to affect survivorship or reproductive participation. Infectious agents observed among adult BONY in open environments include anchor worms, ich, and the Asian tapeworm (Flagg 1982; Hamman 1982; Bozek et al. 1984; Marsh 1985; Tyus et al. 1999; Hansen et al. 2006, 2007; Mueller 2006; Bestgen et al. 2008; Pacey and Marsh 2008a; Portz 2009; Archdeacon et al. 2010; Sykes 2011; Linder et al. 2012; Marsh et al. 2013a). The relationship between BONY adult disease rates and mortality in hatcheries (Pacey and Marsh 2008a; Portz 2009) does not provide an indicator of the strength that this relationship would have outside of hatcheries. Water conditions and exposures to infectious agents are too different between the two settings. The causal relationship therefore warrants low ratings for both magnitude and understanding for both life-stage outcomes.

3. *Foraging*: Analyses of stomach contents and field observations indicate that BONY adults feed on plant litter; aquatic macrophytes; phytoplankton and zooplankton; macroinvertebrates, such as aquatic insect adults and larvae, and crayfish; terrestrial insects that may fall or land on the water; and small vertebrates such as bullfrog larvae and small fish (Vanicek and Kramer 1969; Tyus and Minckley 1988; Lenon et al. 2002; USFWS 2002a; Marsh and Schooley 2004; Mueller 2006; Reclamation 2008; Marsh et al. 2013a). The proportion of larger prey in their diet increases and the proportion of plant matter decreases as BONY increase in size (Mueller 2006). Field observations indicate that they feed mostly at night (Mueller 2006; Marsh et al. 2013b, 2013a) and that they may feed on RASU eggs and their own eggs (Mueller 2006). They feed on different foods in different environments, indicating wide dietary flexibility (USFWS 2002a; Marsh and Schooley 2004). BONY adult morphology, specifically its subterminal mouth position, suggests adaptation to both benthic and open-water feeding (Mueller 2006). Adult BONY must forage to survive; the causal relationship therefore warrants a high rating for magnitude. However, the relationship warrants a low rating for understanding: the relationship between feeding and survival is a basic ecological principle, but there do not appear to be any studies assessing whether low rates of foraging success among BONY adults reduce survivorship or reproductive participation.

4. *Mechanical stress*: The literature does not suggest that established BONY adults experience levels of mechanical stress sufficient to affect their survivorship in LCR open environments. However, the impacts of mechanical stress from scientific study on survivorship are a matter of concern. For example, data on impacts of handling in hatcheries (Sykes 2013) and in the field (Mueller 2006) indicate that mortality does occur from mechanical stress and that it can take as long as 48 hours for surviving stressed individuals to return to a normal state. BONY are also reported to be attracted to fishing lures, again resulting in mechanical stress (Mueller 2006). Nevertheless, the relationship warrants a rating of only medium for magnitude for both life-stage outcomes: The circumstances in which established BONY adults may become mechanically stressed are limited in space and time (e.g., due to fishing encounters or scientific study) and do not cause mortality in all individuals. The relationship for life-stage survival warrants a rating of high for understanding because of the frequent documentation of the ways in which handling can result in mechanical stress to adult BONY. However, the relationship for reproductive participation warrants a rating of low for understanding because the topic has received no specific attention.

5. *Predation*: This is the most commonly proposed cause of the observed poor survivorship among BONY prior to the start of augmentation efforts (Bozek et al. 1984; USFWS 1990, 2002a; Minckley 1991; Minckley et al. 2003; Mueller 2005) and the subsequent poor survival of BONY adults stocked into the system (Lentsch et al. 1995; Minckley et al. 2003; Christopherson et al. 2004; Ward and Hilwig 2004; Brunson and Christopherson 2005; Marsh and Pacey 2005; Modde and Haines 2005; Mueller et al. 2006, 2007; Mueller 2005, 2006, 2007; Reclamation 2006, 2008; Bestgen et al. 2008; Kesner et al. 2008, 2010a, 2010b; Pacey and Marsh 2008b; Portz 2009; Karam and Marsh 2010; Karam et al. 2013; Ward and Figiel 2013). As noted for other BONY life stages, aquatic, avian, and terrestrial fauna able or known to prey on BONY are abundant, widespread, and active year round in the LCR ecosystem and include non-native aquatic predators with different gape-size limitations and/or different predatory behaviors than those present among the native aquatic predators among which BONY evolved. Observations of BONY remains in stomach contents of predators (Bestgen et al. 2008; Karam and Marsh 2010) and the effects of introductions of specific predators into isolated ponds previously free of these predators (e.g., Christopherson et al. 2004; Mueller 2005, 2006) strongly point to predation as a major cause of BONY adult mortality in the system. The major, rapid decline of BONY along the LCR in the 1930s also followed the introduction of several major predators—specifically channel catfish and largemouth bass (see chapter 4)—but preceded the period of construction of the major dams along the LCR, which inundated large stretches of former shoreline and backwater wetlands. In fact, BONY numbers along the LCR initially increased following the filling of Lakes Mohave and Mead (Mueller 2005). For life-stage survival, this causal relationship warrants a high rating for magnitude and understanding. For reproductive participation, this relationship warrants a high rating for magnitude but a low rating for understanding. Other than through the effects of high adult mortality per se, there are no data on how predation affects BONY adult reproductive participation.

6. *Thermal stress*: The literature does not suggest that established BONY adults experience levels of thermal stress sufficient to affect their survivorship or rate of reproductive participation. However, thermally stressful conditions may simply be rare in the present-day system, especially in isolated ponds with highly regulated water conditions. BONY adults in hatcheries appear relatively insensitive to variation in water temperature, within fairly broad ranges of tolerance, suggesting a similar insensitivity of adult BONY in all settings (see chapter 4) Pacey and Marsh 2008a; Portz 2009). Consequently, the causal relationship warrants a low rating for magnitude and a medium rating for understanding for both life-stage outcomes.

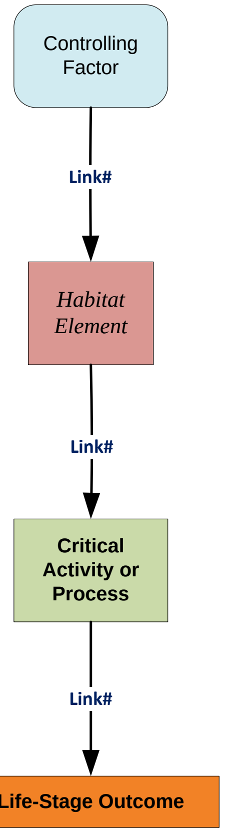
The CEM also identifies several critical biological activities or processes as affecting the two outcomes of this life stage indirectly through their effects on the six biological activities or processes with direct impacts listed above (figure 6). Most notably:

- Competition for food items and habitat (e.g., cover) among established BONY adults and between them and other species may affect foraging success and predator avoidance for this life stage.

- Foraging success provides established BONY adults with the energy to enable them to swim more effectively.

- Unsuccessful predatory attacks may also cause mechanical stress (wounding) among established BONY adults.

- Swimming abilities among established BONY adults affect their capacities to avoid or move away from potentially hazardous conditions of all kinds, forage effectively, and navigate among mesohabitats. Established BONY adults exhibit a range of defensive and avoidance behaviors in response to predator activity, including hiding in geomorphic and vegetative cover (Mueller 2006; Marsh et al. 2013b). Covers used (see "Resting," chapter 3) include dark interstices among cobbles and boulders, bedrock crevices and overhangs, dense emergent and overhanging vegetation, and floating vegetation mats. Defensive behaviors include schooling and "scrumming" (Mueller 2006). In fact, as noted above, schooling not associated with spawning first appears among fry and juveniles and has been reported for all subsequent age classes in both hatchery settings and ponds (Hamman 1982; Mueller et al. 2003, 2004; Mueller 2006).



Link Magnitude

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

Link Understanding

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

Link Predictability

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

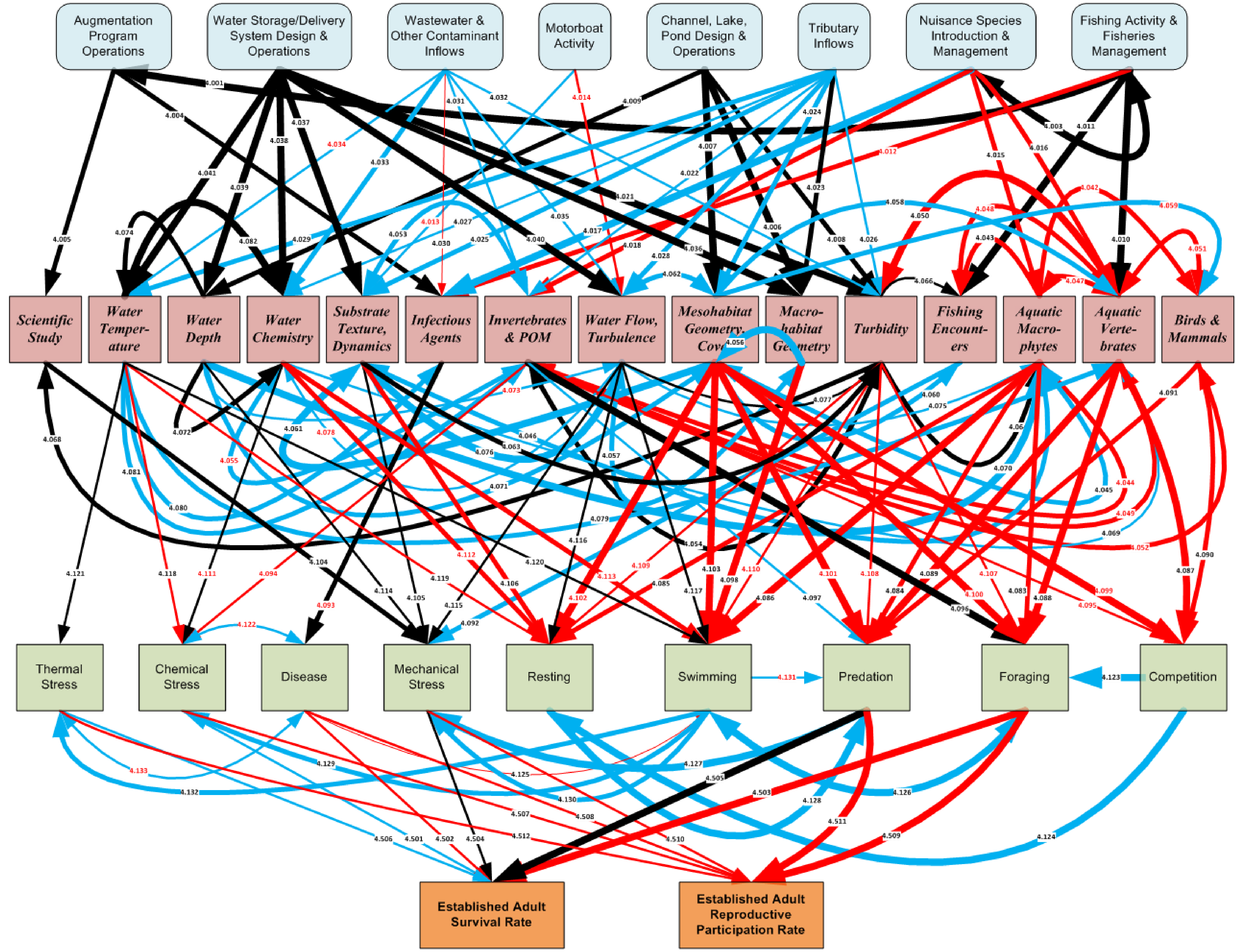


Figure 6.—BONY life stage 4 – established adults.

BONY LIFE STAGE 5 – SPAWNING ADULTS

As described in chapter 2, this life stage covers adults that move to spawning sites to participate in spawning. The component begins when would-be spawners leave their normal territories to move toward spawning sites and ends when these individuals return to their normal territories. The life stage has two life-stage outcomes: (a) S_{SP}, the rate of survival of spawning adults to return to the adult population following spawning, and (b) R_{SP}, the rate of production of fertilized eggs (fertility rate) at spawning sites.

BONY spawn as early as their second year (Age–1), after achieving a body size of ≈ 100 mm TL, but more commonly first spawn in their third year (Age–2) (USFWS 2002a; Mueller 2006; Pacey and Marsh 2008a; Reclamation 2008). Females > 100 mm TL can express eggs and can carry eggs massing up to 20–30 percent of total body weight. The number of eggs produced per female in the LCR, estimated from egg mass, increases with body mass (Hamman 1982, 1985). As noted in chapter 1, BONY female fecundity in the LCR averages approximately 30,000–50,000 ova per kilogram of body mass (Hamman 1985; Marsh 1985). The timing of spawning coincides roughly with the arrival of water temperatures in the range of 18–20 °C (Minckley 1991; Mueller 2006). BONY spawning outside hatcheries takes place in distinct settings visited specifically for spawning (USFWS 2002a; Mueller 2006; Reclamation 2008).

BONY readily spawn in an almost endless variety of natural and artificial settings, sometimes interfering with hatchery efforts to control breeding (Mueller 2006; Pacey and Marsh 2008a; Kesner et al. 2010a, 2010b). Only a few investigators have observed BONY spawning in natural settings (e.g., Minckley 1991; Mueller 2006). Common features of all spawning sites include a relatively uniform range of substrate particle sizes free of silt and other fine sediment and a location adjacent to deeper water (Mueller 2006; Kesner et al. 2010a, 2010b). Consequently, BONY spawning sites may lie immediately adjacent to normal feeding and resting habitat, as investigators observed in Cibola High Levee Pond (Mueller 2006) and suspected to have occurred in Imperial Pond 2 (Kesner et al. 2010b). BONY spawning therefore may involve little or no travel, requiring only minutes or, at most, a very few days of travel time over distances of no more than 10 km per day (Mueller 2006). Spawning occurs over a timespan of seconds to minutes. Several males cluster around each individual female during spawning, and the females broadcast their eggs over the substrate (Minckley 1991; Mueller 2006). Males and females also “fin” over the area of release, from close to the substrate surface, driving the eggs into the substrate. Other BONY, reportedly not the spawners (Mueller 2006), charge into the broadcast areas and push their snouts into the substrate to locate and consume the eggs. However, this activity also churns the substrate, hiding at least some of the eggs from consumption (Mueller 2006).

The CEM, shown in figure 7, identifies 6 (of 11) critical biological activities or processes affecting the two outcomes for this life stage, presented here in alphabetical order. The list does not include foraging, which the literature suggests is not a significant activity during the brief spawning cycle:

1. *Chemical stress*: The CEM recognizes this relationship as a theoretical possibility affecting both life-stage outcomes. The literature presents no evidence BONY spawning adults experience levels of chemical stress sufficient to affect their survivorship or fertility. The CEM recognizes this relationship only because the possible detrimental effects of pollution on BONY in general was a historic concern in the literature (e.g., USFWS 2002a; Minckley et al. 2003). However, studies of the LCR have not supported this larger concern. The causal relationship for both life-stage outcomes therefore warrants a low rating for magnitude but also a low rating for understanding given the absence of systematic observations concerning chemical stress among spawning adults or adults prior to the spawning season.

2. *Disease*: The literature includes no reports of infections specifically in BONY spawning adults sufficient to affect their survivorship or fertility. The relationship between BONY adult disease rates and mortality in hatcheries (Pacey and Marsh 2008a; Portz 2009) does not provide an indicator of the strength that this relationship would have outside of hatcheries. Water conditions and exposures to infectious agents are too different between the two settings. The causal relationship therefore warrants low ratings for both magnitude and understanding for both life-state outcomes.

3. *Mechanical stress*: The literature provides no information on whether BONY spawning adults experience levels of mechanical stress sufficient to affect their survivorship or fertility outside of hatcheries. It appears that scientists avoid disturbing BONY during spawning, and encounters with fishing equipment presumably are unlikely as well. Consequently, the relationship warrants a rating of low for magnitude for both life-stage outcomes. In turn, the relationship for life-stage survival warrants a rating of high for understanding because of the frequent documentation of the ways in which handling can result in mechanical stress to adult BONY coupled with the limited opportunity for mechanically stressful encounters during spawning. In contrast, the relationship for fertility warrants a rating of low for understanding because the topic has received no specific attention.

4. *Predation*: Predation during spawning, as during any life stage, would significantly lower life-stage survival and fertility. However, the literature provides little documentation on predation during spawning. Spawning can occur in shallows and may involve dense aggregation (see chapter 2),

which may make spawning BONY particularly vulnerable to predation, including by birds (Mueller 2006). Gobalet and Wake (2000) suggested that indigenous peoples along the LCR harvested aggregations of spawning BONY by driving them into littoral, shallow-water weirs. The relationship for both life-stage outcomes therefore is rated high for magnitude and low for understanding.

5. *Swimming*: The BONY spawning cycle involves several specific swimming activities, including recognizing suitable spawning sites, navigating and swimming to and from these sites, aggregating at these sites, and the act of spawning itself. The success of BONY in engaging in these swimming activities therefore strongly determines the rate of survival of the spawning adults and their spawning success (fertility). The relationship, therefore, is rated high for magnitude for both life-stage outcomes; however, it is also rated low for understanding for several reasons. First, the details of what conditions trigger BONY to travel to spawning sites and what kinds of sites they select for spawning are not well understood. BONY spawn without difficulty at hatcheries, from which some information on site preferences might be obtained. However, BONY at hatcheries spawn on completely artificial surfaces, for which natural analogs are not readily apparent. Second, observations of BONY spawning site characteristics often use only qualitative descriptive terms such as "gravel" or "coarse," making it difficult to identify preferred properties by comparing sites to each other, especially sites used versus ignored for spawning. Third, BONY preferences for spawning habitat and spawning site fidelity are topics of ongoing investigations funded under the LCR MSCP. Specifically, studies are ongoing under Work Tasks C25, Imperial Ponds Native Fish Research; C40, Genetic and Demographic Studies to Guide Conservation Management of Razorback Sucker and Bonytail in Off-Channel Habitats; and C41, Role of Artificial Habitat in Survival of Razorback Sucker and Bonytail (Reclamation 2014). Additionally, the cues that BONY use to navigate to and from spawning sites are not known nor are the reasons why or the degree to which BONY form dense aggregates at individual spawning (versus forming clumps only immediately during spawning) sites.

6. *Thermal stress*: Water temperature appears to be the dominant environmental cue triggering spawning (see chapters 2, 4, and "Eggs and Early Larvae" in chapter 6). Spawning BONY that encounter temperatures increasingly outside the optimal range for spawning may fail to spawn, reducing fertility. In the extreme, encounters with excessively warm or cold temperatures conceivably could affect metabolic rates and therefore survival as well. However, thermal extremes sufficient to affect BONY fitness are rare in the present-day system, and as noted for other life stages, BONY fitness in hatcheries does not appear to be affected by at least moderate variations in water temperature. The relationship for

life-stage survival therefore is rated low for magnitude and medium for understanding. In contrast, the relationship for fertility is rated medium for both magnitude and understanding. The literature documents the vulnerability of BONY fertility to departures from the optimal temperature range for spawning. However, the spatial scale for such departures in the present-day system will be only medium, affecting only waters that are not highly regulated for temperature (i.e., along the main stem rather than in isolated, highly managed ponds), and such departures will be infrequent given their dependence on river regulation and air temperatures. Additionally, the literature does not document the frequency and intensity of departures from the optimal temperature range across potential BONY spawning habitat along the LCR.

The CEM also identifies two critical biological activities or processes that affect the two outcomes of this life stage indirectly through their effects on the six biological activities or processes with direct impacts listed above (figure 7). Most notably:

- Unsuccessful predatory attacks may also cause mechanical stress (wounding) among established BONY adults.

- Swimming abilities among spawning BONY affect their capacities to avoid or move away from potentially hazardous conditions of all kinds. At the same time, as noted above, BONY aggregation behavior at spawning sites may increase their vulnerability to predation.

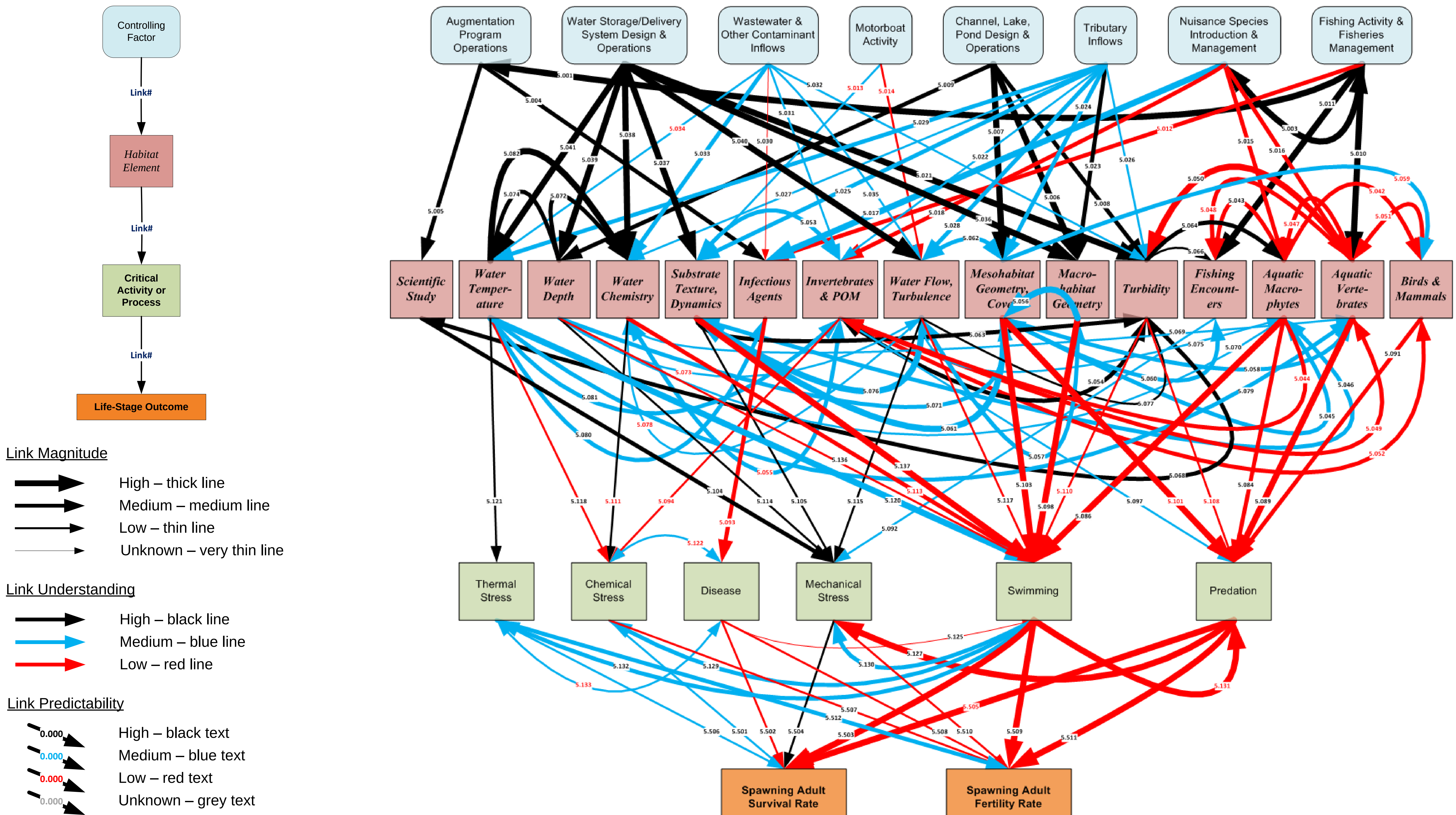


Figure 7.—BONY life stage 5 – spawning adults.

Chapter 7 – Causal Relationships Across All Life Stages

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

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

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

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

Table 7.—Direct effects of critical biological activities and processes on life-stage outcomes (number of life stages in which relationship occurs)

Life-stage outcomes → / ↓ Critical biological activities and processes	Egg and early larval survival rate	Fry and juvenile survival rate	Newly stocked adult survival rate	Established adult survival rate	Established adult reproductive participation rate	Spawning adult fertility rate	Spawning adult survival rate
Chemical stress	1	1	1	1	1	1	1
Competition							
Disease	1	1	1	1	1	1	1
Drifting		1					
Egg settling and adhesion	1						
Foraging		1	1	1	1		
Mechanical stress	1	1	1	1	1	1	1
Predation	1	1	1	1	1	1	1
Resting							
Swimming						1	1
Thermal stress	1	1	1	1	1	1	1

Table 7 indicates the following important (medium- or high-magnitude) direct effects of critical biological activities or processes on life-stage outcomes:

- Predation activities and rates in the LCR and off-channel refuges are proposed to directly affect all seven life-stage outcomes, reducing survivorship in all life stages, the rate of established adult participation in reproduction, and spawning adult fertility.

- Foraging activities and their rates of success in the LCR and off-channel refuges are proposed to directly affect survivorship among fry and juveniles, newly stocked adults, and established adults, and the established adult reproductive participation rate with high magnitude. Foraging is proposed to have no effect on survivorship among early larvae or spawning adults.

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

- The success rate for egg settling and adhesion is proposed to directly affect egg and early larval survival with high magnitude.

- Drifting is proposed to directly affect survivorship among fry during their journey from natal sites to nursery habitat with moderate magnitude.

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

EFFECTS OF CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES ON EACH OTHER

Several critical biological activities and processes help shape other critical biological activities and processes, thereby influencing life-stage outcomes indirectly across the five BONY life stages. Table 8 shows the number of life stages in which each critical biological activity or process directly affects one or more other critical biological activities or processes and the average magnitudes of these effects. Each relationship between one critical activity or process and another is again color coded to indicate the average magnitude (High, Medium, Low, Unknown) of the relationship. Bi-directional relationships are noted in table 8. Two critical biological activities or processes have no direct effect on any other critical biological activities or processes.

Table 8.—Direct effects of critical biological activities and processes on other critical biological activities and processes (number of life stages in which relationship occurs)

Affected critical biological activity or process ➔ / **➔ Causal critical biological activity or process**	Chemical stress	Competition	Disease	Drifting	Egg Settling and adhesion	Foraging	Mechanical stress	Predation	Resting	Swimming	Thermal stress
Chemical stress			5*								
Competition						3			3		
Disease										4	
Drifting						1		1	1		
Egg settling and adhesion											
Foraging										3*	
Mechanical stress											
Predation					1*		5				
Resting								3			
Swimming	4	1		1		2	4	4	2		4
Thermal stress			5*								

* Indicates that a relationship is bi-directional.

Table 8 indicates the following important (medium- or high-magnitude) direct effects of critical biological activities or processes on other critical biological activities or processes:

- Competition is proposed to affect BONY foraging and resting in the LCR and off-channel refuges with high magnitude because BONY appear to face an abundance of competitors for both food materials and resting habitat.

- Drifting is proposed to affect BONY predation in the LCR and off-channel refuges with medium magnitude because the length of drift pathways for fry journeying from their natal sites to nursery habitat affects the duration of their exposure to predators in the open water.

- BONY foraging and swimming in the LCR and off-channel refuges are proposed to affect each other with high magnitude among BONY fry, juveniles, and adults because BONY in these age classes must swim effectively to forage, and the foraging provides the fuel that they need for swimming. Swimming affects foraging with high magnitude, but not vice versa, among BONY early larvae and spawning adults because foraging does not play a strong role in supporting swimming activity during these latter two life stages.

- Predation is proposed to affect the rate of BONY egg settling and adhesion, and vice versa, with high magnitude. Predators can disturb and consume eggs as they settle and begin to adhere, and the slower the settling rate and/or greater the distance that BONY eggs must fall to settle into the substrate, the greater the opportunities for their consumption by predators.

- Predation is also proposed to affect the rate of mechanical stress among BONY in the LCR and off-channel refuges with high magnitude. BONY that escape predator attacks may suffer from wounding.

- Resting activities are proposed to affect predation rates among BONY in the LCR and off-channel refuges with high magnitude. BONY able to find suitable cover from predators suffer less predation.

- Swimming activities are proposed to affect the likelihood of chemical, mechanical, and thermal stress among BONY in the LCR and in its off-channel refuges with medium magnitude. BONY avoid these three forms of stress by swimming away from potentially stressful conditions to the extent that circumstances allow.

- Swimming activities are proposed to affect the distances, duration, and success of drifting among BONY fry along the LCR and in its off-channel refuges with high magnitude. BONY fry swim in and out of currents to control their efforts to move from their natal sites to nursery habitat.

- Swimming activities are proposed to affect the ability of BONY to find suitable resting habitat along the LCR and in its off-channel refuges with medium magnitude.

EFFECTS OF HABITAT ELEMENTS ON CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES

The 17 habitat elements presented in chapter 4 have similar influences on the 11 critical biological activities and processes (chapter 3) across all BONY life stages. Table 9 shows the number of life stages in which each habitat element directly affects one or more critical biological activities or processes. Each relationship between a habitat element and a critical activity or process is again color coded to indicate the average magnitude (High, Medium, Low, Unknown) of the relationship. Bi-directional relationships are noted in table 9.

Table 9.—Direct effects of habitat elements on critical biological activities and processes (number of life stages in which relationship occurs)

Critical biological activities and processes → **↓ Habitat element**	Chemical stress	Competition	Disease	Drifting	Egg settling and adhesion	Foraging	Mechanical stress	Predation	Resting	Swimming	Thermal stress
Aquatic macrophytes						3		5	3	4	
Aquatic vertebrates		3				3		5			
Birds and mammals		3						5			
Fishing encounters							4				
Infectious agents			5								
Invertebrates and particulate organic matter	5	3				3		5			
Macrohabitat geometry				1						4	
Mesohabitat geometry/cover		3		1		3		5	3	5	
Post-rearing transport and release	1						1				1
Pre-release conditioning	1		1			1		1	1	1	1
Scientific study					1		5				
Substrate texture/dynamics					1		5		3	1	
Turbidity						3		5	3	5	
Water chemistry	5								3	5	
Water depth							5			1	
Water flow/turbulence				1	1		5		3	5	
Water temperature	5								3	5	5

Table 9 indicates the following important (medium- or high-magnitude) direct effects of habitat elements on critical biological activities or processes:

- The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophyte assemblage are proposed to affect foraging, predation, and resting across 3–5 life stages with medium magnitude. Aquatic macrophytes provide BONY with cover and foraging opportunities and also provide cover for predators. The spatial distribution of aquatic macrophytes beds also affects the distances that BONY must swim between such sheltering locations.

- The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of the aquatic vertebrate assemblage are proposed to affect competition, foraging, and predation across 3–5 life stages with consistently high magnitude. The aquatic vertebrate assemblage comprises the main pool of species that compete with and prey on BONY, and BONY also prey on smaller aquatic vertebrates.

- The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the bird and mammal assemblages are proposed to affect competition and predation across 3–5 life stages with consistently medium magnitude. The bird and mammal assemblages comprises additional but smaller pools of species that may compete with and/or prey on BONY.

- The types, abundance, distribution, and activity of infectious agents affect the incidence of disease across all five life stages with consistently medium magnitude.

- The taxonomic, functional, and size composition; abundance; spatial and temporal distributions; and activity level of the invertebrate assemblage and the abundance and nutritional quality of particulate organic matter (invertebrates and particulate organic matter) affect foraging by BONY fry, juveniles, and adults with high magnitude. The BONY diet includes invertebrates and particulate organic matter.

- The types, abundance, and spatial and temporal distributions of aquatic macrohabitats affect drifting by fry with medium magnitude and affect swimming by BONY fry, juveniles, and adults with consistently high magnitude. Macrohabitat geometry determines the geography of currents and swimming distances along the LCR.

  The types, abundance, and spatial and temporal distributions of aquatic mesohabitats and cover provided by these habitats affect drifting patterns for BONY fry with medium magnitude and affect BONY fry, juvenile, and adult foraging, predation, resting, and swimming dynamics with consistently high magnitude.

- The types and extent of pre-release conditioning of reared BONY physiology and behavior are known to affect six critical activities or processes for newly stocked adults. Specifically, pre-release conditioning is proposed to have medium-magnitude effects on the incidence of chemical and thermal stress among newly stocked BONY and high-magnitude effects on their foraging, predation, resting, and swimming dynamics. The CEM also proposes that pre-release conditioning affects the incidence of disease among the newly stocked adults, but with unknown magnitude.

- The abundance, spatial distributions, and stability of substrate textures affect swimming behaviors (spawning site selection) and egg settling and adhesion with high magnitude. This habitat element also affects resting, a critical biological activity or process for BONY fry, juveniles, and adults, with medium magnitude.

- The magnitudes and horizontal, vertical, and temporal distributions of water chemistry parameters affect resting site selection by BONY fry, juveniles, and adults with medium-average magnitude.

- The magnitudes and horizontal, vertical, and temporal distributions of water flow velocity and turbulence affect egg settling and adhesion with medium magnitude and affect drifting by fry with high magnitude.

- The magnitudes and horizontal, vertical, and temporal abundance and distributions of water temperatures affect BONY swimming behaviors in all life stages with medium-average magnitude. The average effect of water temperature on swimming, however, masks important variation: it has, on average, a low effect on swimming for all but one life stage, spawning adults, for which it has a high-magnitude effect. The latter effect arises from the high importance of water temperature in triggering spawning and in constraining fertility.

EFFECTS OF HABITAT ELEMENTS ON EACH OTHER

Several habitat elements help shape other habitat elements, thereby influencing critical biological activities and processes indirectly across all BONY life stages. Table 10 shows the number of life stages in which each habitat element directly affects one or more other habitat elements. Each relationship between one habitat element and another is again color coded to indicate the average magnitude (High, Medium, Low, Unknown) of the relationship. Bi-directional relationships are noted in table 10.

Table 10.—Direct effects of habitat elements on other habitat elements (number of life stages in which relationship occurs)

Habitat element 1 → / ↓ Habitat element 2	Aquatic macrophytes	Aquatic vertebrates	Birds and mammals	Fishing encounters	Infectious agents	Invertebrates and particulate organic matter	Mesohabitat geometry/cover	Scientific study	Substrate texture/dynamics	Turbidity	Water chemistry	Water flow/turbulence	Water temperature
Aquatic macrophytes			5	4		5	5*		5*				
Aquatic vertebrates	5*			4		5*				5*			
Birds and mammals		5*				5*							
Invertebrates and particulate organic matter									5*	5*	5*		
Macrohabitat geometry							5					5*	
Mesohabitat geometry/cover		5	5	4					5			5*	
Substrate texture/dynamics										5			
Turbidity	5			4				5					
Water chemistry		5											
Water depth	5						5				5	5	5
Water flow/turbulence	5								5	5	5		
Water temperature		5			5	5					5		

* Indicates that a relationship is bi-directional.

Table 10 indicates the following important (medium- or high-magnitude) direct effects of habitat elements on other habitat elements. Five habitat elements—fishing encounters, infectious agents, post-rearing transport and release method, pre-release conditioning, and scientific study—have no direct effects on any other habitat elements.

- The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophyte assemblage are proposed to affect birds and mammals, fishing encounters, invertebrates and particulate organic matter, mesohabitat geometry/cover, and substrate texture/dynamics in 4–5 life stages with medium magnitude. The latter two relationships are bi-directional: both mesohabitat geometry/cover and substrate texture/dynamics are proposed to affect aquatic macrophytes in all five life stages as well, again with medium magnitude.

- The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of the aquatic vertebrate assemblage are proposed to affect fishing encounters, and invertebrates and particulate organic matter in 4–5 life stages with consistently medium magnitude. The latter relationship is bi-directional. Additionally, the taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of the aquatic vertebrate assemblage are proposed to affect turbidity, and vice versa, with high magnitude in all five life stages.

- The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the bird and mammal assemblages are proposed to affect aquatic vertebrates and invertebrates and particulate organic matter in all five life stages with, on average, medium magnitude. Both relationships are bi-directional.

- The taxonomic, functional, and size composition; abundance; spatial and temporal distributions; activity level of the invertebrate assemblage; and the abundance and nutritional quality of particulate organic matter are proposed to affect substrate texture/dynamics, turbidity, and water chemistry in all five life stages with medium magnitude. All three relationships are bi-directional.

- The types, abundance, and spatial and temporal distributions of aquatic macrohabitats are proposed to affect mesohabitat geometry/cover in all five life stages with consistently high magnitude. Additionally, the types, abundance, and spatial and temporal distributions of aquatic macrohabitats are proposed to affect water flow/turbulence in all five life stages with high magnitude and vice versa.

- The types, abundance, and spatial and temporal distributions of aquatic mesohabitats and cover provided by these habitats are proposed to affect aquatic vertebrates, birds and mammals, fishing encounters, and water flow/turbulence in 4–5 life stages with medium magnitude. The last of these four relationships is bi-directional. Additionally, types, abundance, and spatial and temporal distributions of aquatic mesohabitats and cover provided by these habitats are proposed to affect substrate texture/dynamics in all five life stages with high magnitude.

- The abundance, spatial distributions, and stability of substrate textures are proposed to affect turbidity in all five life stages with medium magnitude.

- The magnitude and spatial and temporal distributions of turbidity are proposed to affect aquatic macrophytes and scientific study in all five life stages with medium magnitude.

- The spatial and temporal distributions of water depth are proposed to affect aquatic macrophytes, invertebrates and particulate organic matter, water chemistry, and water temperature in all five life stages with medium magnitude.

- The magnitudes and horizontal, vertical, and temporal distributions of water flow velocity and turbulence are proposed to affect substrate texture/dynamics in all five life stages with high magnitude.

- The magnitudes and horizontal, vertical, and temporal abundance and distributions of water temperatures are proposed to affect aquatic vertebrates, infectious agents, and invertebrates and particulate organic matter in all five life stages with medium magnitude. Additionally, water temperature is proposed to affect water chemistry in all five life stages with high magnitude.

EFFECTS OF CONTROLLING FACTORS ON HABITAT ELEMENTS

The eight controlling factors discussed in chapter 5 have the same direct effects on the same habitat elements across all life stages. Table 11 shows the magnitudes of direct influence of the 8 controlling factors on the 17 habitat elements identified in the CEM. The structure of table 11 is the same as for table 6, but table 11 shows the magnitudes of the relationships instead of just their presence/absence. Each relationship between a controlling factor and a habitat element is again color coded to indicate the average magnitude (High, Medium, Low, Unknown) of the relationship.

Table 11.—Direct effects of controlling factors on habitat elements (number of life stages in which relationship occurs)

Controlling factor → / **↓ Habitat element**	Augmentation program operations	Channel, lake, and pond design and operations	Fishing activity and fisheries management	Motorboat activity	Nuisance species introduction and management	Tributary inflows	Wastewater and other contaminant inflows	Water storage-delivery system design and operations
Aquatic macrophytes					5			
Aquatic vertebrates			5		5			
Birds and mammals								
Fishing encounters			4					
Infectious agents	5		5		5		5	
Invertebrates and particulate organic matter					5	5	5	
Macrohabitat geometry		5				5		5
Mesohabitat geometry/cover		5				5		
Post-rearing transport and release methods	1							
Pre-release conditioning	1							
Scientific study	5							
Substrate texture/dynamics				5		5		5
Turbidity		5				5	5	5
Water chemistry						5	5	5
Water depth		5						5
Water flow/turbulence				5		5	5	5
Water temperature						5	5	5

Table 11 indicates the following important (medium- or high-magnitude) direct effects of controlling factors on habitat elements. These relationships affect all five life stages except where otherwise noted:

- Augmentation program operations are proposed to affect post-rearing transport and release methods with high magnitude among newly stocked adults and to affect infectious agents and scientific study with medium magnitude.

- Channel, lake, and pond design and operations are proposed to affect macrohabitat geometry and mesohabitat geometry and cover with high magnitude and to affect turbidity and water depth with medium magnitude.

- Fishing activity and fisheries management are proposed to affect aquatic vertebrates with high magnitude and to affect fishing encounters and infectious agents with medium magnitude.

- Nuisance species introduction and management are proposed to affect infectious agents with high magnitude and to affect aquatic macrophytes, aquatic vertebrates, and invertebrates and particulate organic matter with medium magnitude.

- Tributary inflows are proposed to affect macrohabitat geometry, mesohabitat geometry and cover, substrate texture/dynamics, water flow/turbulence, and water temperature with medium magnitude.

- Wastewater and other contaminant inflows are proposed to affect water chemistry with medium magnitude.

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

One controlling factor also shapes habitat elements indirectly, through its effects on two other controlling factors:

- Fishing activity and fisheries management affects augmentation program operations with high magnitude. Many species introduced as sport fishes, or as bait or forage for sport fisheries—either officially by agencies or unofficially by fishermen—prey on or compete with BONY. Introductions of these non-native predators and competitors into isolated water bodies that formerly lacked them have devastated BONY numbers in these locations. The augmentation program therefore tries to take into account the distributions of non-native predators in selecting LCR locations for releases.

  Fishing activity and fisheries management also affects nuisance species introduction and management with high magnitude. Some species intentionally introduced as bait and forage for sport fisheries—either officially by agencies or unofficially by fishermen—have become nuisance species. Recreational fishers and State agency fishery management activities also have been and likely continue to be unintentional sources of nuisance species such as quagga and zebra mussel that "hitchhike" into the LCR on boating and fishing equipment or in containers used intentionally to transport sport, forage, or bait species. Further, fisheries managers and sport fishermen may respond to the presence/absence of nuisance species in the system by introducing other species to control them.

POTENTIALLY INFLUENTIAL CAUSAL RELATIONSHIPS WITH LOW UNDERSTANDING

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

Tables 12 and 13 identify those relationships that the CEM proposes have high magnitude but low understanding. Table 12 identifies such relationships specifically in which the causal agent is a habitat element, and table 13 identifies such relationships specifically in which the causal agent is a critical biological activity or process. No high-magnitude but low-understanding relationships exist in which the causal agent is a controlling factor. Tables 12 and 13 indicate the number of life stages for which the CEM proposes the relationship. Bi-directional relationships are noted in table 8.

Table 12.—High magnitude but poorly understood relationships between habitat elements and other variables (number of life stages in which relationship occurs)

Affected condition ➔ **➔ Causal agent: Habitat element**	Competition	Drifting	Egg settling and adhesion	Foraging	Predation	Resting	Swimming	Turbidity
Aquatic macrophytes							4	
Aquatic vertebrates	3			2	5			5*
Macrohabitat geometry							3	
Mesohabitat geometry/cover	3			3	5	3	4	
Pre-release conditioning				1	1	1	1	
Substrate texture/dynamics			1				1	
Water flow/turbulence		1						

Table 12 indicates consistently low levels of understanding of the ways in which two habitat elements affect multiple critical biological activities and processes across most of the five BONY life stages:

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

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

Additionally, table 12 indicates low levels of understanding of how the taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophytes assemblage affect swimming behaviors among BONY fry, juveniles, and adults. Finally, table 12 indicates a low level of understanding of the ways in which pre-release conditioning may affect foraging, predation, and resting and swimming behaviors among newly stocked BONY adults.

Table 13 indicates consistently low levels of understanding of the ways in which three critical biological activities or processes, foraging, predation, and swimming behaviors affect several other critical biological activities and processes as well as all seven life-stage outcomes across the five BONY life stages.

Table 13.—High-magnitude but poorly understood relationships between critical biological activities or processes and other variables (number of life stages in which relationship occurs)

Affected condition ➔ **🡻 Causal agent: Critical activity or process**	Drifting	Mechanical stress	Predation	Egg and early larval survival rate	Fry and juvenile survival rate	Newly stocked adult survival rate	Established adult survival rate	Established adult reproductive participation rate	Spawning adult fertility rate	Spawning adult survival rate
Foraging					1	1	1	1		
Predation		1		1				1	1	1
Swimming	1		1						1	1

Chapter 8 – Discussion and Conclusions

This document presents a CEM for BONY. The purpose of this model is to help Reclamation, LCR MSCP, identify areas of scientific certainty versus uncertainty concerning BONY ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the indicators used to measure BONY habitat and population conditions. The CEM addresses the BONY population along the river and lakes of the LCR and other protected areas.

The CEM methodology involves six core steps:

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

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

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

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

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

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

The BONY conceptual ecological model identifies five life stages: eggs and early larvae, fry and juveniles, newly stocked adults, established adults, and spawning adults. Life-stage outcomes consist of the survival rate for each life stage, the established adult reproductive participation rate, and the spawning adult fertility rate. The BONY CEM identifies 11 critical biological activities and processes that affect one or more of these life-stage outcomes: chemical stress, competition, disease, drifting, egg settling and adhesion, foraging, mechanical stress, predation, resting, swimming, and thermal stress.

In turn, the CEM identifies 17 habitat elements, the abundance, composition, or other properties of which affect 1 or more critical activities or processes: aquatic macrophytes, aquatic vertebrates, birds and mammals, fishing encounters, infectious agents, invertebrates and particulate organic matter, macrohabitat geometry, mesohabitat geometry/cover, post-rearing transport and release methods, pre-release conditioning, scientific study, substrate texture/dynamics, turbidity, water chemistry, water depth, water flow/turbulence, and water temperature.

Finally, the CEM identifies eight controlling factors, the dynamics of which affect the abundance, composition, or other properties of one or more habitat elements: augmentation program operations; channel, lake, and pond design and operations; fishing activity and fisheries management; motorboat activity; nuisance species introduction and management; tributary inflows; wastewater and other contaminant inflows; and water storage-delivery system design and operations.

The assessment of the causal relationships among these controlling factors, habitat elements, critical biological activities and processes and life-stage outcomes indicates the following strong (high-magnitude) causal relationships. These results specifically refer to the BONY population along the river and the lakes of the LCR and other protected areas.

KEY IMPACTS OF CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES

Predation rates affect all seven life-stage outcomes with high magnitude. Understanding of the effects of predation on life-stage outcomes is rated low for four life-stage outcomes: egg and early larval survival rate, established adult reproductive participation rate, spawning adult survival rate, and spawning adult fertility rate. Understanding of the effects of predation on life-stage outcomes is rated medium for fry and juvenile survival and newly stocked adult survival and rated high for established adult survival.

Foraging success directly affects four life-stage outcomes with high magnitude but low understanding: established adult reproductive participation, established adult survival, newly stocked adult survival, and fry and juvenile survival. Foraging success also affects life-stage outcomes indirectly through its high-magnitude/medium-understanding impact on swimming ability.

Swimming abilities and behaviors directly affect two life-stage outcomes with high magnitude but low understanding: spawning adult survival and spawning adult fertility. Additionally, swimming abilities and behaviors affect life-stage outcomes indirectly through their high-magnitude effects on drifting (low understanding) and foraging (medium understanding) and their medium-magnitude effects on predation, resting, and thermal stress (all with medium understanding).

Three other direct effects are evident. Egg settling and adhesion has a high-magnitude effect on egg and early larval survival, with high understanding. Drifting has a medium-magnitude effect on fry and juvenile survival, with low understanding. Thermal stress, in this case the potential for altered thermal cues for spawning, directly affects spawning adult fertility with medium magnitude and medium understanding. The present-day system is so highly regulated, both within the river and in its isolated ponds, that temperature extremes formerly associated with the seasons and with flood pulses no longer occur.

Important indirect effects of critical biological activities and processes on life-stage outcomes include the impact of predation on egg settling and adhesion (high magnitude, high understanding), the impact of swimming abilities on drifting behavior (high magnitude, low understanding), and the impacts of competition from other BONY and other species for habitat and food on BONY resting and foraging (both high magnitude, low understanding).

KEY HABITAT ELEMENTS

Based on their high or medium magnitudes, on average, across the five life stages, four habitat elements strongly directly affect critical biological activities or processes (in alphabetical order): aquatic macrophytes, aquatic vertebrates, macrohabitat geometry, and mesohabitat geometry/cover. Based on the number of other critical biological activities or processes they affect, the most influential habitat elements directly affecting critical biological activities or processes are (in alphabetical order): aquatic macrophytes, invertebrates and particulate organic matter; mesohabitat geometry/cover; turbidity; water flow/turbulence; and water temperature.

Based on their average high or medium magnitudes, six habitat elements strongly *indirectly* affect critical biological activities or processes (in alphabetical order):

aquatic macrophytes, invertebrates and particulate organic matter; macrohabitat geometry; mesohabitat geometry/cover; water depth; and water temperature. Based on the number of other habitat elements they affect, the most influential habitat elements that *indirectly* affect critical biological activities or processes by strongly affecting other habitat elements are (in alphabetical order): aquatic macrophytes, aquatic vertebrates, mesohabitat geometry/cover, turbidity, water depth, water flow/turbulence, and water temperature.

Most of the causal relationships between one habitat element and another have high or medium understanding, reflecting the stability of knowledge of how different physical conditions in aquatic ecosystems affect each other. For example, the ways in which water depth affects water temperature or affects the availability of habitat for aquatic macrophytes or aquatic invertebrates are well understood in the field of aquatic ecology in general. In contrast, most of the direct causal relationships between habitat elements and critical biological activities and processes for BONY have low understanding. For example, the ways in which pre-release conditioning may affect BONY resting, foraging, or swimming behaviors or vulnerability to predation are not well understood. Similarly, knowledge is weak concerning the ways in which aquatic macrophytes, substrate texture, or mesohabitat geometry may affect BONY foraging, resting, or vulnerability to predation; or concerning the ways in which the abundance and composition of the aquatic vertebrate or aquatic invertebrate assemblages may affect the rates of competition that BONY experience when foraging or seeking cover (resting).

Only three causal relationships between habitat elements and critical biological activities or processes have medium or high understanding: the effects of water flow/turbulence on egg settling and adhesion (medium understanding), the effects of mesohabitat geometry/cover on drifting (medium understanding), and the effects of the abundance and composition of invertebrates and particulate organic matter on BONY foraging (high understanding).

KEY CONTROLLING FACTORS

Water storage-delivery system design and operations has high-magnitude, well-understood effects on turbidity, water chemistry, water depth, macrohabitat geometry, water flow/turbulence, water temperature, and substrate texture/dynamics. Channel, lake, and pond design and operations have high-magnitude effects on macrohabitat geometry and on mesohabitat geometry/cover and medium-magnitude effects on turbidity and water depth. All effects of channel, lake, and pond design and operations are well understood. Tributary inflows have medium-magnitude effects on macrohabitat geometry, water flow/turbulence, water temperature, substrate texture/dynamics, and mesohabitat geometry/cover. Understanding is high for the first of these five effects of tributary inflows, and medium for the other four. Nuisance species introduction and management has medium-magnitude, poorly understood effects on invertebrates and particulate organic matter, aquatic vertebrates, and aquatic macrophytes. Fishing activity and fisheries management directly affects aquatic vertebrates with high magnitude and high understanding. Wastewater and other contaminant inflows affect water chemistry with medium magnitude and understanding.

Augmentation program operations affect pre-release conditioning with low magnitude and medium understanding. This link is included as a “significant” relationship because the topic of pre-release conditioning for BONY has received attention as a possible way to reduce mortality among BONY released from hatcheries into the LCR and its isolated ponds.

Only one controlling factor affects life-stage outcomes indirectly through its effects on other controlling factors. Fishing activity and fisheries management has a high-magnitude, well-understood effect on nuisance species introduction and management. Specifically, unregulated fishing activities have accidentally introduced, and in the future may additionally introduce, nuisance species to the LCR ecosystem. Similarly, fishing activity and fisheries management has a high-magnitude, well-understood effect on augmentation program operations. The augmentation program must take into account the types and extent of fishing and fisheries management activities throughout the LCR in determining where to release hatchery-reared BONY, where fishing activities could interfere with augmentation program efforts, and how recreational fishers might help provide useful information on BONY (e.g., through creel surveys).

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ATTACHMENT 1

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

OVERVIEW OF METHODOLOGY

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

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

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

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

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

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

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

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

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

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

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

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

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

(1) The effect of one controlling factor on another

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

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

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

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

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

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

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

Conceptual Ecological Models as Hypotheses

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

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

Characterizing Causal Relationships

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

(1) The character and direction of the effect

(2) The magnitude of the effect

(3) The predictability (consistency) of the effect

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

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

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

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

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

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

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

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

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

Conceptual Ecological Model Documentation

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

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

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

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

Link Attribute Ratings, Spreadsheet Fields, and Diagram Conventions

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

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

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

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

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

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

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

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

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

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

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

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

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

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

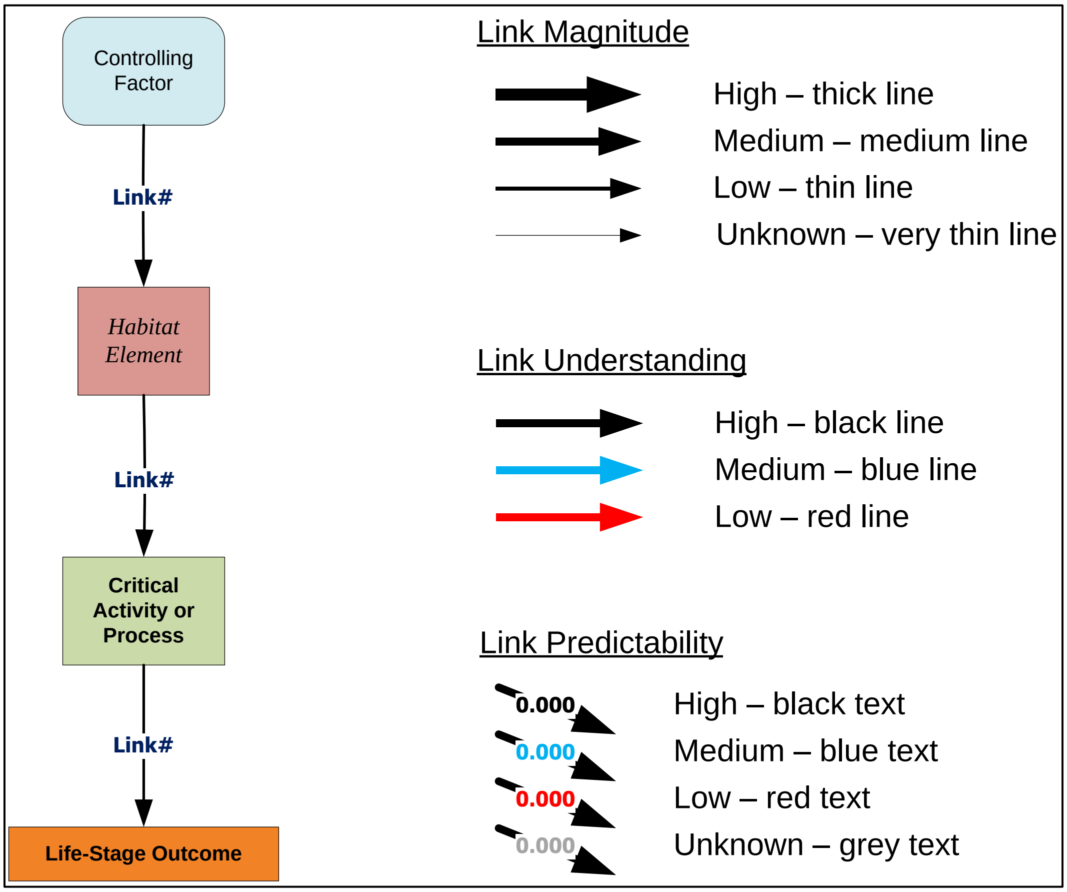

Figure 1-1.—Conventions for displaying cause and effect nodes, linkages, link magnitude, link understanding, and link predictability.

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