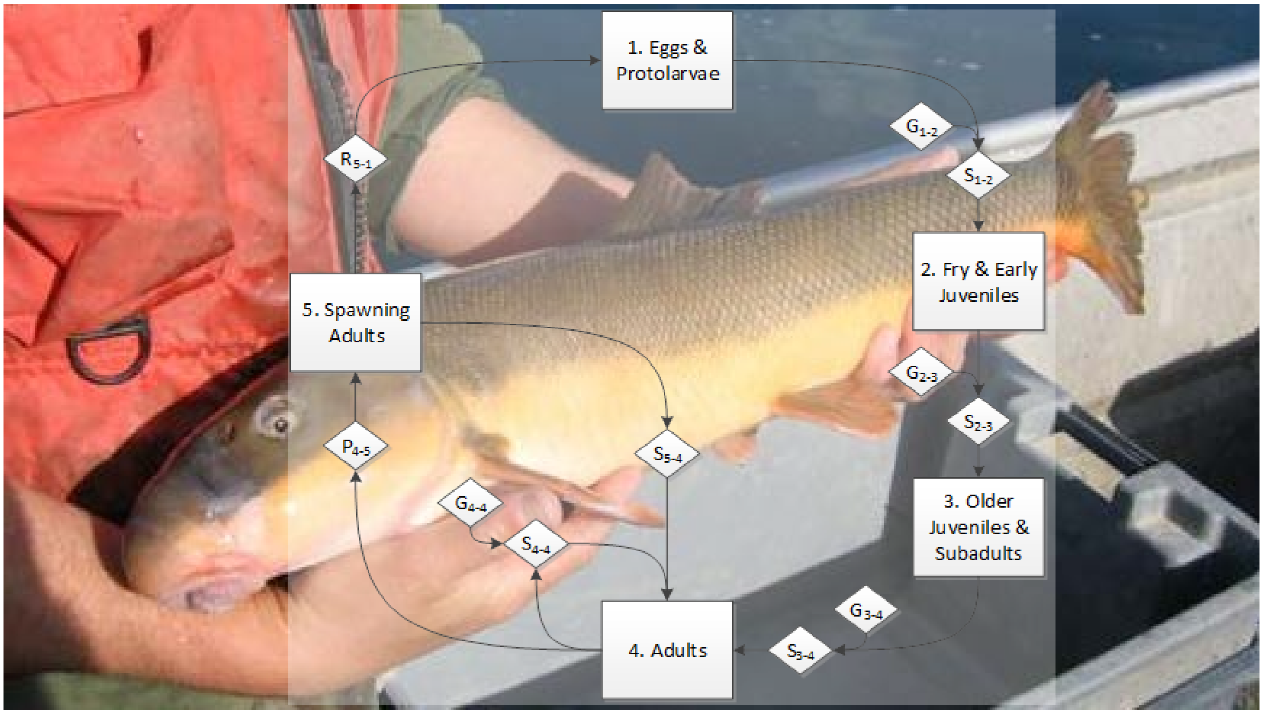
Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

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

2018 Updates



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U.S. DEPARTMENT OF THE INTERIOR
BUREAU OF RECLAMATION

March 2019

Lower Colorado River Multi-Species Conservation Program
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Lower Colorado River
Multi-Species Conservation Program

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

2018 Updates

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Multi-Species Conservation Program
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March 2019

Braun, D.P. 2019. Flannelmouth Sucker (*Catostomus latipinnis*) (FLSU) Basic Conceptual Ecological Model for the Lower Colorado River, 2018 Updates. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada, by Sound Science, LLC, Boise, Idaho under contract No. R16PC00028.

ACRONYMS AND ABBREVIATIONS

AGFD	Arizona Game and Fish Department
BBCA	Big Bend Conservation Area
BONY	bonytail (*Gila elegans*)
CAP	critical activity or process
CEM	conceptual ecological model
CF	controlling factor
DNA	deoxyribonucleic acid
DO	dissolved oxygen
EPA	Environmental Protection Agency
FLSU	flannelmouth sucker (*Catostomus latipinnis*)
HE	habitat element
IPCA	Imperial Ponds Conservation Area
km	kilometer(s)
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
LSO	life-stage outcome
mm	millimeter(s)
n	number
NISIC	National Invasive Species Information Center
NRC	National Research Council
PADCNR	Pennsylvania Department of Conservation and Natural Resources
pH	potential of hydrogen (expressing acidity or alkalinity)
PIT	passive integrated transponder
POM	particulate organic matter
RASU	razorback sucker (*Xyrauchen texanus*)
Reclamation	Bureau of Reclamation
TL	total length
UCRB	Upper Colorado River Basin
USDA	U.S. Department of Agriculture
UDWR	Utah Department of Water Resources
USFWS	U.S. Fish and Wildlife Service

Symbols

°C	degrees Celsius
>	greater than
%	percent

CONTENTS

Tables

Figures

Foreword

This report provides an update to the original conceptual ecological model (CEM) prepared for the Lower Colorado River Multi-Species Conservation Program (LCR MSCP) for the flannelmouth sucker (*Catostomus latipinnis*) (FLSU) (Braun 2015a). This update incorporates information reported in publications and presentations at professional meetings since the completion of the original FLSU conceptual ecological model, and information from the professional experiences of LCR MSCP staff and other experts. An updated version of the CEM workbook incorporates the new information. This report constitutes is an appendix to the original FLSU conceptual ecological model. The full CEM report, including its life-stage diagrams, has not been updated.

This update does not change the overall structure of the FLSU conceptual ecological model. However, this update adds four new life-stage outcomes—egg and protolarval growth, fry and early juvenile growth, older juvenile and subadult growth, and adult growth. The inclusion of growth as an outcome for these life stages follows the practice established in recent quantitative life history models for other native and non-native fishes in the Colorado River, including the humpback chub (*Gila cypha*) (Yackulic et al. 2014) and brown trout (*Salmo trutta*) (Runge et al. 2018).

The structure of this report (update) follows the structure of the original FLSU conceptual ecological model report. Specifically, it presents and documents updates to chapters 1–6. It does not include updates to the original Executive Summary or to chapters 7–8 because these sections were not updated.

This update provides a list of all literature cited in the updates to chapters 1–6. In addition, it documents all changes made to the names of CEM components in order to standardize terminology across all CEMs.

This update both explicitly and implicitly identifies possible research and monitoring questions concerning gaps in knowledge that may bear on adaptive management of FLSU in the lower Colorado River. These questions may or may not reflect the current or future goals of the LCR MSCP. The CEM identifies these questions only for the purpose of informing LCR MSCP decisionmakers and are in no way meant as a call for the Bureau of Reclamation to undertake research to fill the identified knowledge gaps.

Updates to Chapter 1 – Introduction

Flannelmouth suckers (*Catostomus latipinnis*) (FLSU) continue to occupy only a single portion of the lower Colorado River (LCR), specifically the section of Reach 3 between Davis Dam and Lake Havasu. The updated assessment of causal relationships—as with the assessment for the original FLSU conceptual ecological model (Braun 2015a)—consequently mostly concerns this section of the river. However, FLSU abundance has increased during the current decade in the Colorado River in the Lower Grand Canyon down to Lake Mead (Albrecht et al. 2016; Bezzerides and Bestgen 2002; BIO-WEST, Inc., and American Southwest Ichthyological Researchers 2017; Kegerries et al. 2015, 2016, 2017) and has either held steady or increased in the Colorado River inflow, Echo Bay, and the Virgin River/Muddy River inflow areas of Lake Mead itself (Kegerries et al. 2016, 2017; Mohn et al. 2016). The closely related and ecologically similar razorback sucker (*Xyrauchen texanus*) (RASU) has experienced active recruitment over the past decade in these same portions of the Grand Canyon and Lake Mead (BIO-WEST., Inc. 2017; U.S. Fish and Wildlife Service [USFWS] 2018). FLSU captured in Lake Mead in the Colorado River inflow, Echo Bay, and the Virgin River/Muddy River inflow areas in fact include FLSU-RASU hybrids and larvae indicative of *in situ* spawning (Kegerries et al. 2016, 2017; Mohn et al. 2016). The increasing abundance of FLSU in the Lower Grand Canyon and steady or increasing abundance in Lake Mead, and the parallel active recruitment of RASU in these same waters, provide additional information for updating the FLSU conceptual ecological model (see also Braun 2017).

FLANNELMOUTH SUCKER REPRODUCTIVE ECOLOGY

The updates to chapters 2–4 address several aspects of FLSU ecology, including reproductive ecology. The revised information particularly concerns the following:

- *Spawning triggers*: See the updated discussion of spawning triggers in chapter 2 and the updated discussion of water flow and turbulence in chapter 4.

- *Hybridization*: See the updated discussion in chapters 2 and 3, and the addition of a new habitat element, "Genetic Diversity," in chapter 4.

- *Predation*: See the updated discussion of predation in chapter 3 and the updated discussions in chapter 4 concerning five habitat elements that affect predation, specifically “Aquatic Macrophytes,” “Aquatic Vertebrates,” “Birds and Mammals,” “Mesohabitat Structure,” and “Turbidity.”

- *Avoidance of lacustrine habitat by FLSU subadults and adults*: See the updated discussion of spawning triggers in chapter 2, the updated discussions of long-distance movement and swimming in chapter 3, and the updated discussion of water flow and turbulence in chapter 4.

- *FLSU use of aquatic macrophytes and turbidity as cover*: See the updated discussions of aquatic macrophytes, aquatic vertebrates, birds and mammals, mesohabitat structure, and turbidity in chapter 4.

CONCEPTUAL ECOLOGICAL MODEL PURPOSES

This update does not propose any changes to this section of chapter 1. However, when the CEMs are fully updated, chapter 1 should be revised to indicate that the CEM methodology followed here is a crucial foundation for carrying out effects analyses as described by Murphy and Weiland (2011, 2014) and illustrated by Jacobson et al. (2016).

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

No change.

Updates to Chapter 2 – FLSU Life Stage Model

This update adds four new life-stage outcomes to the FLSU conceptual ecological model focused on growth and standardizes the names of all life-stage outcomes for consistency. Table 1 and figure 1 are updated accordingly. The updated version of figure 1 also appears in the cover illustration for the present document.

Table 1.—Update of table 1, FLSU life stages and life-stage outcomes

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

Specifically, this update adds "Egg and Protolarval Growth," "Fry and Early Juvenile Growth," "Older Juvenile and Subadult Growth," and "Adult Growth" as life-stage outcomes. These changes recognize the importance of growth as an outcome parallel to survival. Growth includes egg maturation; increasing body size among larvae, juveniles, subadults, and adults (as measured by total length [TL]); maturation of morphology, including various transformations in larval, juvenile, subadult, and adult morphology; and the temporary development (expression) of secondary sexual characteristics among adults. Growth also includes the allocation of resources to maintain or recover body condition (e.g., as measured by Fulton's condition factor, K) (Froese 2006; Nash et al. 2006) during or following episodes of stress and associated loss of body mass. The inclusion of growth as an outcome for these life stages follows the practice established in recent quantitative life history models for other native and non-native fishes in the Colorado River, including the humpback chub (*Gila cypha*) (Yackulic et al. 2014) and brown trout (*Salmo trutta*) (Runge et al. 2018).

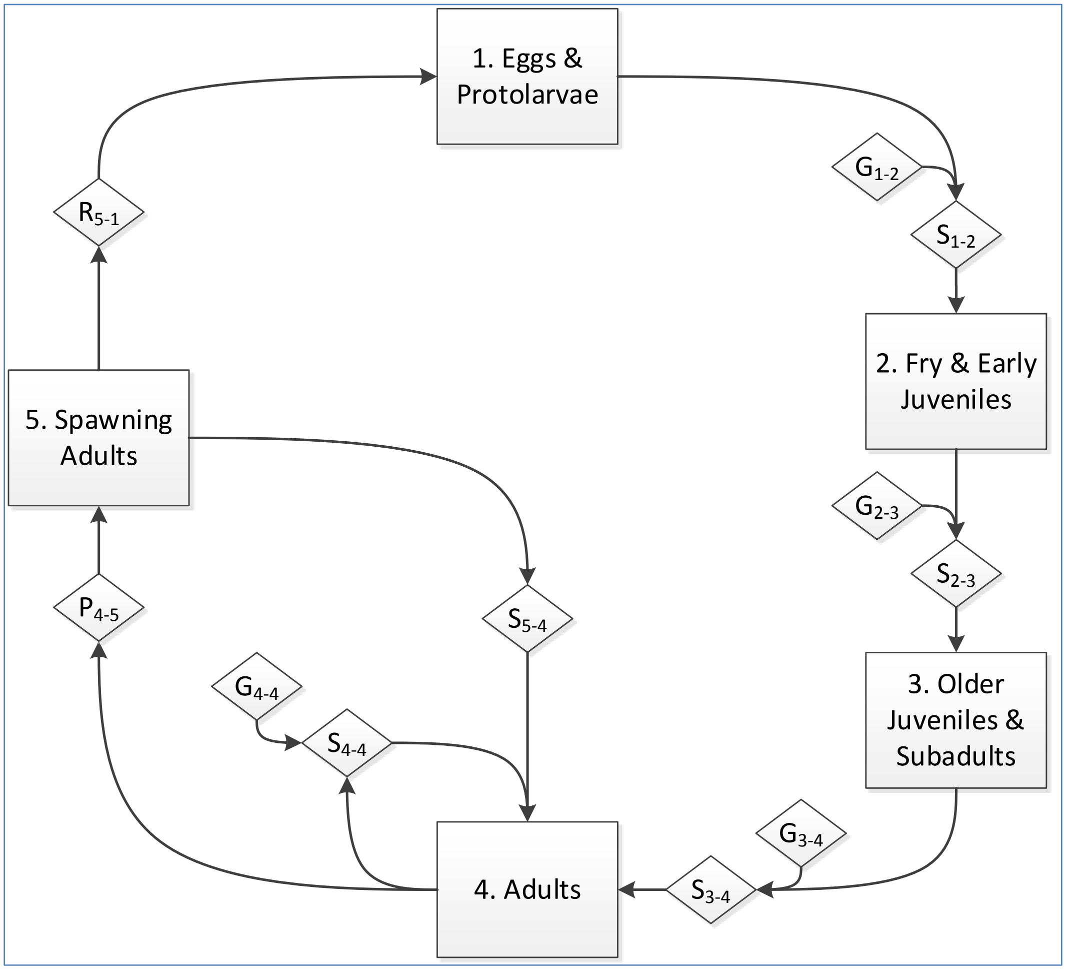

Figure 1.—Proposed updated FLSU life history model.
Squares indicate life stages; diamonds indicate life-stage outcomes. Life-stage outcomes are rates, as follows:
G_{1-2} = growth, eggs and protolarvae; S_{1-2} = survival, eggs and protolarvae; G_{2-3} = growth, fry and early juveniles; S_{2-3} = survival, fry and early juveniles; G_{3-4} = growth, older juveniles and subadults; S_{3-4} = survival, older juveniles and subadults; S_{4-4} = annual survival, adults; G_{4-4} = annual growth, adults; P_{4-5} = participation of adults in spawning activity; S_{5-4} = survival, spawning adults; and R_{5-1} = fertility, spawning adults.

Numerous habitat elements affect growth in each FLSU life stage through the effects of these habitat elements on critical biological processes, including thermal and chemical stress, and foraging success, as discussed in the original FLSU conceptual ecological model (Braun 2015a). In turn, inhibited growth among FLSU—as with inhibited growth in any fish species (Froese 2006; Hayes et al. 2017)—is likely to affect FLSU critical biological activities and processes and other life-stage outcomes in several ways, as also documented in the original FLSU conceptual ecological model (Braun 2015a): Individual eggs and protolarvae, fry, juveniles, and subadults that grow more slowly will spend more time in their respective life stages, increasing their exposure to threats specific to that life stage, including predation. To the extent that FLSU adult vulnerability to predation depends in part on body size, as discussed in the original FLSU conceptual ecological model, adults that grow more slowly will spend more time as smaller adults, potentially increasing their exposure to predation. Further, as a result of their relative physical weakness, individual protolarvae, fry, juveniles, subadults, and adults that do not experience growth sufficient to maintain or quickly return to good body condition following some disturbance may be more vulnerable to predation or less able to avoid or escape extreme flow disturbances compared to less impaired individuals in these same life stages. Finally, individual adults that do not experience growth sufficient to maintain good body condition may be less likely to participate in spawning or, if they do participate, may contribute less to reproductive output at the spawning site(s) they visit.

This update does not include growth as a life-stage outcome for spawning adults. Spawning FLSU, as with spawning individuals among fish species in general, presumably lose body mass as a result of their energy expenditures and potentially also their loss of appetite and/or diversion from foraging activity while participating in spawning (Froese 2006; Nash et al. 2006). However, recovery from this stress occurs after spawning, once the participating individuals start their return to the general adult population. Otherwise, individuals in this brief life stage are simply adults in all other respects, and the CEM assumes that growth (gain-loss) during this life stage is not ecologically relevant. The CEM recognizes that the condition of spawning adults conceivably could affect their survival. However, hypothetically, individuals in poor condition simply may not participate in spawning in the first place—a subject that has not been studied with respect to FLSU.

This update also standardizes the names of FLSU life-stage outcomes as follows: (1) “Survival Rate” changes to “Survival” for all four life stages; (2) “Adult Reproductive Output Rate” changes to “Adult Reproductive Output”; and (3) “Spawning Adult Fertility Rate” changes to “Spawning Adult Fertility.”

Finally, this update recognizes new information to include in the basic description of the “Spawning Adult” life stage. The original FLSU conceptual ecological model (Braun 2015a) noted that changes in water temperature rather than changes in river discharge appear to provide the dominant cue initiating spawning along a given reach of the Colorado River and its tributaries (Bezzerides and Bestgen 2002; Lower Colorado River Multi-Species Conservation Program [LCR MSCP] 2008; Minckley and Marsh 2009; Rees et al. 2005; Zelasko et al. 2011). The original FLSU conceptual ecological model specifically cited the fact of FLSU spawning along the LCR between Davis Dam and Lake Havasu (Best and Lantow 2012a, 2012b) as evidence that FLSU can spawn in response to factors other than changes in discharge: This section of the river experiences highly unnatural discharges from Davis Dam, dictated by operating rules to meet requirements for water storage and use unrelated to the natural flow regime.

This update takes similar note of evidence for *in situ* spawning of FLSU in Lake Mead—the presence of FLSU-RASU hybrids and FLSU larvae in the Colorado River inflow area, Echo Bay, and the Virgin River/Muddy River inflow area (Kegerries et al. 2016, 2017; Mohn et al. 2016). This evidence similarly indicates that FLSU spawning need not depend on the occurrence of specific discharge conditions. Further, Klein et al. (2017) examined statistical relationships of FLSU growth and recruitment to multiple indicators of the hydrologic regime along the upper Green, lower Green, Strawberry, and White Rivers, Utah, in the Upper Colorado River Basin (UCRB) Their results showed that none of the hydrologic indicators or combinations of these indicators reliably predicted variation in FLSU growth or recruitment.

Evidence presented by Fraser et al. (2017), in turn, strengthens the case for changes in water temperature as the most important spawning cue. Specifically, Fraser et al. (2017) present evidence that changes in water temperature cue the movement of FLSU into tributaries to spawn in the UCRB. The original FLSU conceptual ecological model also noted that the spawning of FLSU between Davis Dam and Lake Havasu (Best and Lantow 2012a, 2012b) does not contradict the identification of thermal change as the dominant spawning trigger: This section of the river does experience a modified thermal regime. However, the temperature of the air strongly affects the temperature of the water, resulting in relatively natural annual and diurnal patterns of temperature *variation* around the modified annual and daily average temperatures along this section of the river (Braun 2015a). Appropriate *changes* in water temperature consequently do occur to trigger spawning. No further information has emerged on the possible role of the photoperiod in triggering spawning (Hoffnagle et al. 1999; Robinson et al. 1998).

The description of the “Spawning Adult” life stage in chapter 2 of the original FLSU conceptual ecological model (Braun 2015a) also included information on spawning locations and the distances over which FLSU adults move to reach spawning sites. The original FLSU conceptual ecological model cited Valdez et al. (2000) that ripe adult FLSU may aggregate at or near spawning locations for several weeks prior to spawning. However, the original FLSU conceptual ecological model also noted that the literature does not consistently identify such staging or recognize it as a distinct component of the spawning cycle. Fraser et al. (2017) do not mention any separate staging behavior or any lag in timing between FLSU movement into and spawning in the UCRB tributary they studied.

The original FLSU conceptual ecological model additionally suggested that spawning sites appear to be more widely available to FLSU in the UCRB compared to the situation in the Grand Canyon or between Davis Dam and Lake Havasu. The original FLSU conceptual ecological model followed Holden and Stalnaker (1975) in suggesting that spawning sites may be more widely available in the UCRB simply as a consequence of differences in river morphology.

More recent evidence from Lake Mead and the Grand Canyon suggest that other factors may be at work in determining where or how widely FLSU spawn. As noted above, surveys in Lake Mead have recorded evidence of FLSU spawning in the Colorado River inflow area, Echo Bay, and the Virgin River/Muddy River inflow area (Kegerries et al. 2016, 2017; Mohn et al. 2016). In turn, intensive larval fish surveys in the Grand Canyon, 2014–16, found FLSU protolarvae in almost every one of the sampling segments surveyed above Lake Mead, up to 309 river kilometers (192 river miles) upstream, the upper limit of the survey study area (Gilbert et al. 2017; Kegerries et al. 2016). For example, the 2016 larval fish survey in the Lower Grand Canyon captured FLSU protolarvae during at least one of the five months (March – June, August) of the survey in 30 of these 55 segments. Since FLSU protolarvae have very limited swimming capability, their presence at a sampling location indicates spawning occurred at or above that location. The results of the Lower Grand Canyon larval fish surveys also indicate that, as the season progressed from March to June each year, the zone within which FLSU spawning occurred expanded further upstream every month, with protolarvae present only in approximately the lower half of the study area by April but up to the upstream limit of the study area by June. The presence of FLSU protolarvae all the way up to River Mile 88 in June (309 river kilometers [192 river miles] above Lake Mead, at the Bright Angel Creek confluence) indicates that FLSU spawning also occurred upstream of this location as well. The Lower Grand Canyon study was not designed to identify or enumerate individual FLSU spawning sites. It is not known whether changes in the availability of potential spawning habitat in Lake Mead and the Grand Canyon have improved the ability of FLSU to spawn in these waterbodies or if other factors are at work.

Updates to Chapter 3 – Critical Biological Activities and Processes

CHEMICAL STRESS

The discussion of this critical process is updated as follows:

Hinck et al. (2007, 2008, 2009) and Patiño et al. (2012) found that a variety of metal and synthetic organic compound contaminants are present in the Colorado River main stem, tributary waters, and main stem impoundments in the Lower Colorado River Basin, and in discharges to the Colorado River throughout its entire basin from urban areas and wastewater treatment outflows (see also Dwyer et al. 2005). Further, these same studies found that these contaminants can bioaccumulate in the fish assemblage. The LCR MSCP has long monitored selenium in sediment and the water along the LCR (LCR MSCP 2018) and in 2017 also began monitoring selenium body loads in fishes, macroinvertebrates, and periphyton. The LCR MSCP sampling of fishes and other organisms included samples from the Big Bend Conservation Area (BBCA) in the section of Reach 3 occupied by FLSU (LCR MSCP 2018). The LCR MSCP annual report for the 2017 fiscal year (LCR MSCP 2018) states, "A bluegill whole body sample collected at the BBCA [Big Bend Conservation Area] had a selenium concentration of 13.6 parts per million dry weight, which is above the 8.5 parts per million selenium concentration EPA criterion and above the high-hazard threshold for fishes. Mysid shrimp collected at the BBCA were above the high-hazard threshold for macroinvertebrates. All other invertebrate and fish samples had selenium concentrations lower than the EPA criterion and the moderate threat level threshold."

The findings on bioaccumulation obtained by Hinck et al. (2007, 2008, 2009) and Patiño et al. (2012), and by the LCR MSCP for the BBCA all concern non-native rather than native fishes. However, Walters et al. (2015) examined mercury and selenium bioaccumulation in the Colorado River food web in the Grand Canyon and found elevated levels of both elements in FLSU. The literature therefore documents: (1) a continuing ubiquity of these two contaminants in the food web in the Colorado River ecosystem downstream from the Grand Canyon and Lake Mead (Hinck et al. 2007, 2008, 2009; LCR MSCP 2018; Patiño et al. 2012), (2) the presence of at least selenium along the LCR, including in Reach 3, and (3) a propensity among FLSU to bioaccumulate these contaminants from the food web (Walters et al. 2015). These results suggest that FLSU in the river section of Reach 3 between Davis Dam and Lake Havasu likely experience elevated body loads of both elements; however, FLSU may not necessarily experience significant chemical stress from these body loads.

More generally, FLSU that experience chemical stress presumably lose body mass as a result of their energy expenditures and, potentially, loss of appetite and/or diversion from foraging activity, during avoidance of or recovery from chemical stress, as occurs with fish species in general (Froese 2006; Nash et al. 2006). A study by Hamilton and Buhl (1997) appears to be the only laboratory assessment of FLSU larval susceptibility to the effects of contaminants, specifically mixtures of inorganic contaminants simulating water conditions recorded at different locations along the San Juan River. The watershed of this tributary to the Colorado River has a history of mining waste discharges, contaminated irrigation return flows, and incidences of infected lesions among fishes. The lesions are thought to have been initiated by contact with other stressors "such as high contaminant concentrations, malnutrition, or poor water quality." The study results showed that FLSU larvae were susceptible to harmful effects of various mixtures of dissolved metals, particularly copper and zinc, at concentrations sometimes found in contaminated San Juan River backwaters and tributary reaches. In contrast, results of the study showed that FLSU larvae were relatively unaffected by arsenic, boron, molybdenum, selenate, selenite, uranium, and vanadium. The authors also note that the biological effects of inorganic contaminants can vary with other environmental factors such as water pH, salinity, dissolved oxygen (DO) levels, and temperature. However, the study did not include systematically investigating such interactions.

Variation in water chemistry could also have indirect effects on FLSU. For example, variation in dissolved nutrients could affect rates of primary (autochthonous) production in waters occupied by FLSU (Melis et al. 2010; National Research Council [NRC] 1991; Ohmart et al. 1988), affecting the availability of food items for the species. As noted elsewhere (see "Invertebrates and Particulate Organic Matter," in chapter 4 of Braun [2015a]), toxins released by golden alga (*Prymnesium parvum*) blooms could also harm FLSU in backwaters and other waterbodies with limited water circulation.

This update therefore includes causal links from chemical stress to egg and protolarval growth, fry and early juvenile growth, older juvenile and subadult growth, and adult growth. In turn, as discussed above, the model adds links from these "growth" outcomes to survival for these four life stages and a link from adult growth to spawning participation for this latter life stage. At the same time, the CEM retains direct links from chemical stress to survival and spawning participation because chemical stress can affect these outcomes directly, too, separately from any effects it may have on growth. The CEM also retains links from water chemistry to invertebrate and particulate organic matter (POM) production.

COMPETITION

No change. Competition does affect the new life-stage outcomes related to growth in protolarvae, fry and early juveniles, older juveniles and subadults, and adults. However, these effects occur indirectly through the direct effects of competition on foraging and resting/hiding.

DISEASE

The discussion of this critical process is updated as follows:

Diseased FLSU presumably lose body mass during illness as a result of their energy expenditures and, potentially, loss of appetite and/or diversion from foraging activity, as do diseased individuals among fish species in general (Froese 2006; Nash et al. 2006). This update therefore includes causal links from disease to egg and protolarval growth, fry and early juvenile growth, older juvenile and subadult growth, and adult growth. In turn, as discussed above, the model adds links from these “growth” outcomes to survival for these four life stages and a link from adult growth to spawning participation for this latter life stage. At the same time, the CEM retains direct links from disease to survival and spawning participation because disease can affect these outcomes directly, too, separately from any effects it may have on growth.

DRIFTING

The discussion of this critical activity is updated as follows:

The intensive larval fish surveys in the Grand Canyon, 2014–16 (see “Updates to Chapter 2 – FLSU Life Stage Model”), have found more than just FLSU protolarvae in a majority of the sampling segments surveyed above Lake Mead, up to the upper limit of the survey study area at River Mile 88): The surveys have found every other FLSU larval stage and both fry and early juvenile FLSU as well (Gilbert et al. 2017; Kegerries et al. 2016). The Lower Grand Canyon larval fish survey sampled low-velocity mesohabitat types in every segment and recognized the following low-velocity mesohabitat types: backwater, eddy, embayment, isolated pool, pocket water, pool, shoal, and slackwater (Kegerries et al. 2016).

As noted in the original FLSU conceptual ecological model (Braun 2015a), channel sections along which lateral and reverse currents draw drifting fish larvae out of the main line of downstream flow into low-velocity settings such as shoreline embayments and entrances to backwaters may be termed “interception habitats”—a term developed for application to the drifting of larvae of the endangered pallid sturgeon (*Scaphirhynchus albus*) along the Missouri River (Jacobson et al. 2016). Kinzli and Myrick (2010) present a similar concept for the role of Rio Grande channel shoreline features in intercepting the drifting eggs of the Rio Grande silvery minnow (*Hybognathus amarus*) (see also Worthington et al. 2014). FLSU larvae depend on such interception habitats to convey them into the low-velocity settings that provide nursery habitat or resting/hiding habitat during larval drift to nursery habitat. The results of the recent larval fish surveys in the Grand Canyon thus necessarily indicate not only successful spawning but also successful drifting and settling of the drifting larvae into suitable nursery habitat as well. The majority of the 55 river segments sampled for the Lower Grand Canyon larval fish surveys, along the 309 km (192 river miles) surveyed above Lake Mead, therefore contain both interception habitat and low-velocity habitat where drifting FLSU can rest.

The recent evidence from Lake Mead, from the Colorado River inflow area, Echo Bay, and the Virgin River/Muddy River inflow area (Kegerries et al. 2016, 2017; Mohn et al. 2016) similarly indicates successful FLSU recruitment in the lake as well. The recruitment in the Colorado River inflow and Virgin River/Muddy River inflow areas conceivably could be the result of drift from FLSU populations upstream in the Grand Canyon and Virgin River Basin (see above and Bezzerides and Bestgen 2002). However, Echo Bay in Lake Mead has no such inflow source for drifting FLSU larvae. This latter circumstance raises the possibility that lake currents in Echo Bay were sufficient to convey drifting larvae from spawning to nursery sites or that the spawning occurred in one or more low-velocity settings that also immediately provided suitable nursery habitat, with little or no intervening drift required.

EGG SETTLING AND ADHESION

No change.

FORAGING

The discussion of this critical activity is updated as follows:

FLSU body condition presumably varies with foraging success for all motile life stages that forage (Froese 2006; Hayes et al. 2017; Nash et al. 2006). This update therefore includes a causal link from foraging to egg and protolarval growth, fry and early juvenile growth, older juvenile and subadult growth, and adult growth. This change requires eliminating two types of links included in the original FLSU conceptual ecological model (Braun 2015a): (1) links from Foraging directly to Survival for these four life stages, with the caveat that FLSU protolarvae forage very little and (2) the link from Foraging to Reproductive Participation for Adults. These deleted links are replaced with links from egg and protolarval growth, fry and early juvenile growth, older juvenile and subadult growth, and adult growth to survival for these four life stages, and a link from adult growth to adult reproductive participation.

HYBRIDIZATION

The discussion of this critical process is updated as follows:

Hybridization occurs when two species together produce live offspring that share genetic materials from both parental species. A review by Scribner et al. (2001) identifies the following as potential causes of hybridization among closely related fish species: “external fertilization; weak behavioral isolating mechanisms; unequal abundance of the two parental species; competition for limited spawning habitat; decreasing habitat complexity; and susceptibility to secondary contact between recently evolved forms.” The review also indicates that closely related sympatric species may hybridize simply because they spawn at the same places and times without necessarily competing for limited spawning habitat.

The original FLSU conceptual ecological model (Braun 2015a) summarized numerous studies finding that, across the Colorado River Basin overall, FLSU occasionally hybridize with other catostomids, including native RASU and bluehead suckers (*Catostomus discobolus*), and with non-native white suckers (*C. commersonii*). Neither bluehead suckers nor white suckers occur within the LCR (as compared to the upper Colorado River), let alone specifically within the geographic range of FLSU within the LCR (Bezzerides and Bestgen 2002; Fuller 2018). However, the geographic range of FLSU within the LCR does overlap with that of RASU. As summarized recently (LCR MSCP 2016):

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

Recent fish surveys in Lake Mead and in the Grand Canyon have repeatedly captured FLSU-RASU hybrids (Albrecht et al. 2010a, 2010b; BIO-WEST, Inc., and American Southwest Ichthyological Researchers 2017; Bureau of Reclamation [Reclamation] 2017; Dowling et al. 2014a, 2014b, 2015, 2016; Gilbert et al. 2017; Kegerries and Albrecht 2011, 2013; Kegerries et al. 2016, 2017; Mohn et al. 2016; USFWS 2016; Wolters et al. 2016, 2017). Genetic data indicate past hybridization between the two species affecting the genetic makeup of the present RASU population in Lake Mohave as well (Buth et al. 1987; Marsh et al. 2015). The present review did not locate any reports of FLSU-RASU hybrids captured between Davis Dam and Lake Havasu, the only portion of the LCR where FLSU are present—a section of the river where RASU also are stocked (Marsh et al. 2015; LCR MSCP 2017, 2018).

Conceptual *ecological* models such as the present FLSU conceptual ecological model—as contrasted with conceptual models of gene flow—mostly take into account genetic variation only as it bears on species ecology. Hybridization of FLSU with RASU in the LCR ecosystem poses two kinds of threats to FLSU *ecological* circumstances within the LCR. First, the effective fertility of non-hybrid FLSU suffers when FLSU gametes fertilize or are fertilized by another species. Second, hybrid protolarvae, fry, juveniles, subadults, and adults potentially may compete with non-hybrid FLSU for food or physical habitat. For example, Anderson and Stewart (2007) found that, unlike native catostomids, the non-native white sucker and its hybrids can persist in western Colorado regardless of alterations to the flow regime, giving them an advantage over the native suckers. Studies of the possible demographic and ecological consequences of hybridization between FLSU and RASU are ongoing (Wolters et al. 2016, 2017).

LONG-DISTANCE MOVEMENT

The discussion of this critical activity is updated as follows:

The original FLSU conceptual ecological model identifies long-distance movement as a possible activity for older juveniles and subadults, adults, and spawning adults (Braun 2015a). Hypothetically, FLSU moving over long distances could pass through zones with stressful thermal or hydrologic conditions, increasing their energy expenditures (Underwood et al. 2014; see "Swimming," this chapter), or through zones with inadequate foraging resources, decreasing their energy uptake. Both circumstances therefore could affect growth among older juveniles and subadults, adults, or spawning adults. However, the present review did not locate any reports of FLSU bioenergetics either in relation to long-distance movement or in general.

Further, the original FLSU conceptual ecological model (Braun 2015a) notes that impoundments behind dams may present barriers to FLSU movement, such as movement between the river main stem and tributaries with confluences inundated by a given reservoir. The original FLSU conceptual ecological model specifically noted the following: (1) The currents necessary for FLSU larval drift (Zelasko et al. 2011) dissipate in large impoundments. (2) This loss of drift currents presumably prevents or greatly impedes further downstream movement of the larvae. (3) The shallow, low-velocity environments created at the immediate confluences of rivers with impoundments may provide nursery habitat for FLSU fry arriving from upstream—habitat perhaps similar to the pools that can form at tributary confluences with the main stem Colorado River (Robinson et al. 1998; Zelasko et al. 2011). However, (4) FLSU older juveniles to adults subsequently either avoid impoundments, fail to persist in them, or retreat back upstream even if they initially matured in nursery habitat at an impoundment inflow or if currents or swimming activity brought them into impoundments (Bezzerides and Bestgen 2002; Mueller and Wydoski 2004; Zelasko et al. 2011).

This update takes into account the recent presence, persistence, and reproduction of FLSU in Lake Mead in the Colorado River inflow area, Echo Bay, and the Virgin River/Muddy River inflow area (see chapter 2 and discussion of long-distance movement, above, this chapter). These findings suggest that FLSU in fact do not necessarily find impoundments intolerable. Specifically, the data indicate FLSU movement to Echo Bay from both the Virgin River/Muddy River and Colorado River Inflow areas. Roughly 10 km of open-water lentic habitat separates Echo Bay from the Virgin River/Muddy River inflow area, the nearest perennial inflow. The FLSU present in the Virgin River/ Muddy River inflow area could be from the FLSU population in the Virgin River/ Muddy River Basin (Bezzerides and Bestgen 2002). In 2016, Mohn et al. (2016) recaptured two tagged FLSU-RASU hybrids in Echo Bay that were originally captured and tagged in the Virgin River/Muddy River inflow area. (No deoxyribonucleic acid [DNA] data are yet available to determine whether the FLSU present in Echo Bay are members of this same tributary population or constitute a separate reproductive unit). Similarly, in 2016, Mohn et al. (2016) recaptured two tagged FLSU in Echo Bay that were originally captured and tagged in the Colorado River inflow arm, a distance of roughly 50 km entirely through open water. (No DNA data are yet available to assess the extent of genetic exchange between the FLSU in the Overton and Colorado River Inflow arms of the lake). These findings suggest that FLSU are swimming over distances of 10–50 km within Lake Mead. The literature does not yet provide evidence or suggestions for why FLSU are able to move within Lake Mead with such apparent ease, in contrast to their pattern of avoiding or fleeing lentic waters elsewhere in the Colorado River Basin. Nevertheless, the emerging evidence indicates that impoundments *per se* may not present absolute barriers to FLSU long-distance movement.

MECHANICAL STRESS

The discussion of this critical process is updated as follows:

FLSU that experience mechanical stress presumably lose body mass as a result of their energy expenditures and, potentially, loss of appetite and/or diversion from foraging activity, during avoidance of or recovery from mechanical stress, as occurs with fish species in general (Froese 2006; Nash et al. 2006). This update therefore includes causal links from mechanical stress to egg and protolarval growth, fry and early juvenile growth, older juvenile and subadult growth, and adult growth. In turn, as discussed above (see "Foraging," this chapter), the model adds links from these "growth" outcomes to survival for these four life stages and a link from adult growth to spawning participation for this latter life stage. At the same time, the CEM retains direct links from mechanical stress to survival and spawning participation because mechanical stress can affect these outcomes directly, too, separately from any effects it may have on growth.

PREDATION

The discussion of this critical process is updated as follows:

As noted in the original FLSU conceptual ecological model (Braun 2015a), predation is a normal evolutionary pressure. Prey species evolve behaviors and physical characteristics through natural selection that allow them to persist and even thrive despite predation. However, new information adds to our understanding of the different effects of pre-Euro-American versus present-day predation on FLSU.

As discussed in the original FLSU conceptual ecological model (Braun 2015a), depredation by the Colorado pikeminnow (*Ptychocheilus lucius*) may have been among the selective pressures shaping FLSU reproductive biology. Mueller and Marsh (2002) argue that episodic droughts that greatly reduced native fish abundances in the LCR ecosystem would have selected for the ability of the native prey fishes to reproduce more rapidly and in greater numbers than can the pikeminnow. This difference in reproductive ecology would have allowed the native prey fishes to reach reproductive size/age quickly and in large numbers, producing abundant cohorts of offspring to rebuild population numbers before pikeminnow numbers could fully recover.

At the same time, Mueller and Marsh (2002) suggest that, because they faced only one significant predator—the Colorado pikeminnow—the native prey fishes of the Colorado River Basin did not evolve complex repertoires of behaviors and physical adaptations to predation. Mueller and Marsh (2002) hypothesize that this situation left the native fishes particularly vulnerable to depredation by the numerous non-native aquatic predators introduced by Euro-Americans. However, this hypothesis may overstate the simplicity of the predatory environment prior to Euro-American impacts. Specifically, the hypothesis does not recognize (1) the potentially large effects of natural predation on native fish *larvae* by other native fishes and by other aquatic vertebrates and invertebrates and (2) perhaps more importantly, the potential effects of predation on fish larvae, juveniles, and adults by *birds*. Both of these effects would be more likely in the shallow, low-velocity environments in which FLSU often occur. Each of these two potential sources of predation would have exerted its own evolutionary pressures on the behaviors and physical characteristics of all native prey fishes.

Understanding of avian predation on native fishes along the LCR has expanded significantly since completion of the original FLSU conceptual ecological model (Braun 2015a) through direct monitoring of avian feeding. Much of this monitoring has focused on Laughlin Lagoon, located between Davis Dam and Lake Havasu, the only section of the LCR where FLSU occur. The monitoring at Laughlin Lagoon, using bird roosts equipped with cameras, focused specifically on avian predation on bonytail (*Gila elegans*; BONY): BONY could be stocked into the lagoon after being tagged with passive integrated transponders (PITs), which allowed the investigators to examine the dynamics of avian predation and BONY survival in greater detail (Best et al. 2017; Mueller 2017). Recent information on avian predation on native fishes along the LCR also comes from camera monitoring at the Bill Williams River National Wildlife Refuge and Imperial Ponds Conservation Area (IPCA), and from field observations of avian predation and/or talon and beak injuries to both BONY and RASU in the Havasu National Wildlife Refuge and along Reaches 4–5 (Best 2015; Humphrey et al. 2014, 2015, 2016; Lantow 2017; LCR MSCP 2017; McCall et al. 2017).

Although mostly focused on BONY, these new data streams have implications concerning the possibility of avian predation on FLSU as well. Specifically, the studies in Laughlin Lagoon found that BONY are highly vulnerable to predation by numerous bird species, including (but not limited to) great blue herons (*Ardea herodias*), osprey (*Pandion haliaetus*), and double-crested cormorants (*Phalacrocorax auritus*) (see chapter 4, “Birds and Mammals”). Avian predators consumed a large fraction of the BONY released for the camera monitoring studies at the lagoon.

The findings from Laughlin Lagoon suggest that BONY vulnerability to avian predation results from the fish remaining near the water surface despite the clarity (low turbidity) of the water. FLSU similarly spend significant time near the water surface—in the upper 50 centimeters or less (Braun 2015a)—and the LCR everywhere exhibits low turbidity through the effects of the numerous dams along the system (Braun 2015a). Therefore, one might hypothesize that FLSU would be similarly vulnerable. However, the BONY used to study avian predation at Laughlin Lagoon were reared in hatcheries and released without any pre-release conditioning to the presence of avian predators or any extended period of post-release acclimation to a predator-rich environment. The FLSU in the LCR, in contrast, have lived their entire lives in this predator-rich environment. FLSU that survive in this environment would be likely to have repertoires of avoidance behaviors that the hatchery-reared BONY would not, potentially including behaviors that take into account water clarity.

One might also hypothesize that, at the very least, FLSU adults might be less vulnerable to avian predation than are BONY adults in open environments because FLSU attain larger body sizes than do BONY: FLSU adults today can reach 400–600 millimeters (mm) TL, while BONY adults today typically reach only 300–400 mm TL even in hatcheries (Braun 2015a, 2015b). However, the hypothesis lacks support: There is no evidence for any effect of body size on avian predation on BONY along the LCR. The birds feeding on BONY at Laughlin Lagoon and elsewhere along the LCR (see studies cited above) consume larger and smaller BONY with equal ease. Further, the potential effects of body size would apply only to adult fish. The size range of younger FLSU falls within that of the BONY on which the birds fed so readily at Laughlin Lagoon. Finally, Riedel et al. (2007) found that avian predators at the Salton Sea tended to avoid eating larger fishes and also preferred slender-bodied fishes over deep-bodied ones. The avian predators along the LCR are the same as those around the Salton Sea, and FLSU have a slender body form. Consequently, from the standpoint of body size and shape, it seems likely that FLSU should be highly vulnerable to avian predation between Davis Dam and Lake Havasu.

At the same time, FLSU have repertoires of avoidance behaviors that may help thwart avian predation. FLSU of varying sizes take cover from predators in the interstices in cobble/boulder substrates as well as in stands of aquatic macrophytes, in turbid water, and under overhanging banks and submerged woody debris; may alternatively seek deeper water when turbidity is low; and move out into open waters preferentially at night, when the darkness provides its own cover for their activities (Beland 1953; Best and Lantow 2012a, 2012b, 2015; Bestgen et al. 2011; Budy et al. 2009; Childs et al. 1998; Cross 1975; LCR MSCP 2018; Stone 2010; Weiss 1993). Chapter 4, “Birds and Mammals,” provides further information.

Albrecht et al. (2010c) have identified an increased abundance of emergent vegetation in Lake Mead, associated with declining lake levels, as a possible significant factor in the recent successful spawning and recruitment of RASU in the lake. The present chapter of this update earlier noted the evidence of successful FLSU spawning and recruitment in Lake Mead, and the presence of FLSU-RASU hybrids as evidence of simultaneous spawning of FLSU and RASU at the same sites. These lines of evidence suggest that, if the increased abundance of emergent vegetation in Lake Mead provided effective cover for RASU, it may be doing so for FLSU as well. However, the literature reviewed for this update does not contain any systematic data on the possible effects of aquatic macrophyte cover or turbidity on FLSU vulnerability to predation.

RESTING/HIDING

The discussion of this critical activity is updated as follows:

Formerly named simply “Resting,” the critical activity is renamed “Resting/Hiding” for consistency with other CEMs and to clarify its meaning. Further, the definition of this critical activity is revised to explain the distinction between resting and hiding. Fish may “rest” merely by moving to or staying in locations where they can hold their position without significant expenditures of effort. However, they may also do so in habitat settings in which FLSU can hide themselves from predators and/or secure themselves against hydrologic disturbances that could otherwise displace them. As noted above, FLSU use crevices in substrates, overhanging banks and vegetation, submerged woody debris, emergent aquatic vegetation, and turbid waters for resting/hiding. As also noted in the original FLSU conceptual ecological model (Braun 2015a), FLSU older juveniles, subadults, and adults occupy, feed, and move preferentially at greater depths than do other large fishes of the Colorado River Basin, at least during the day, and move into shallower waters at night (Beyers et al. 2001; Budy et al. 2009; Childs et al. 1998; Karp and Tyus 1990; Weiss 1993). FLSU thus appear to use both deeper waters and the darkness of night as cover as well. (This latter inference may not apply to FLSU larvae.) As noted in the original FLSU conceptual ecological model, the larvae of many native fishes of the Colorado River, following swim-up, seek shelter along shorelines during the day and drift preferentially at night. However, the literature is divided over such diel sheltering among FLSU larvae (Bezzerides and Bestgen 2002; LCR MSCP 2008; Rees et al. 2005; Robinson et al. 1996, 1998).

This update also notes that FLSU resting/hiding behavior in all motile life stages potentially could affect the likelihood of their detection and/or capture during monitoring. This relationship potentially exists because the detection rates of different tracking methods (e.g., PIT tag monitoring) may differ when fishes are at lesser versus greater depth, in open water versus hiding in cover habitat, or moving in or out of turbid waters (see chapter 4, “Turbidity”). The likelihood of capture by different methods (e.g., by electrofishing or various net-based methods) similarly may vary. These relationships are suggested based on evidence from studies of the humpback chub (Yackulic et al. 2018). Conversely, efforts to capture fishes may cause them to flee, resulting in a bi-directional relationship. For example (see chapter 4, “Monitoring, Capture, Handling”), the LCR MSCP (2018) has noted a relationship between FLSU behavior and detection during monitoring. Specifically, telemetric monitoring of sonic-tagged

FLSU released below Davis Dam found that detection of the FLSU with ultrasonic receivers was noticeably more difficult when the FLSU moved into the cover of bulrush (*Schoenoplectus californicus*) stands during the daylight hours. Presumably, the monitoring teams could not move their ultrasonic receivers into these stands of emergent vegetation, and the fish moved far enough into the vegetation to escape the detection radius of the receivers.

SWIMMING

The discussion of this critical activity is updated as follows:

Underwood et al. (2014) tested the swimming performance of FLSU in comparison to that of the closely related bluehead sucker, white sucker, mountain sucker (*Catostomus platyrhynchus*), and longnose sucker (*C. catostomus*), and the unrelated roundtail chub (*Gila robusta*) that can occur in the same waters in the UCRB. The results were similar to those reported by Ward and Hilwig (2004), Ward et al. (2002), and as discussed in the original FLSU conceptual ecological model. These earlier studies found that FLSU are not the strongest swimmers among the large, native fishes of the LCR, exhibiting lower failure velocities in laboratory experiments than either RASU or BONY. Underwood et al. (2014) found that FLSU swimming abilities are most similar to those of the longnose sucker. However, there was relatively little variation in the sizes of the FLSU tested (approximately 250–400 mm TL) compared to the size variation among the other four species tested (e.g., approximately 120–360 mm TL for longnose suckers). This situation limited the ability of the study to assess how FLSU swimming abilities vary with body size.

FLSU swimming performance likely varies with body condition, as is the case with fish species in general (Froese 2006; Nash et al. 2006). The CEM recognizes this as a possible causal relationship for the egg and protolarval, fry and early juvenile, older juvenile and subadult, and adult life stages. However, the literature reviewed for the original FLSU conceptual ecological model or for this update does not directly address this topic.

The original FLSU conceptual ecological model (Braun 2015a) also notes that older juvenile, subadult, and adult FLSU appear to actively flee or avoid lentic waters (Bezzerides and Bestgen 2002; Chart and Bergersen 1992; LCR MSCP 2008; Mueller and Wydoski 2004; Rees et al. 2005). However, the recent presence, persistence, and reproduction of FLSU in Lake Mead in the Colorado River inflow area, Echo Bay, and the Virgin River/Muddy River inflow area (see chapter 2 and the discussion of long-distance movement, above, this chapter) suggest that older juveniles, subadults, and adults in fact do not always find impoundments intolerable.

This update also notes that FLSU swimming behavior in all motile life stages potentially could affect the likelihood of their detection and/or capture during monitoring. This relationship potentially exists—as noted above concerning resting/hiding—because the detection rates of different tracking methods (e.g., PIT tag monitoring) may differ when fish are at lesser versus greater depth, out in open water versus hiding in cover habitat, or moving in or out of turbid waters (see chapter 4, "Turbidity"). The likelihood of capture by different methods (e.g., by electrofishing or various net-based methods) similarly may vary. These relationships are suggested based on evidence from studies of the humpback chub (Yackulic et al. 2018). Conversely, efforts to capture fishes may cause them to flee, resulting in a bi-directional relationship.

THERMAL STRESS

The discussion of this critical process is updated as follows:

FLSU that experience thermal stress presumably lose body mass as a result of their energy expenditures and, potentially, loss of appetite and/or diversion from foraging activity, during avoidance of or recovery from thermal stress, as occurs with fish species in general (Froese 2006; Nash et al. 2006). This update therefore includes causal links from thermal stress to egg and protolarval growth, fry and early juvenile growth, older juvenile and subadult growth, and adult growth. In turn, as discussed above (see "Foraging," this chapter), the model adds links from these "growth" outcomes to survival for these four life stages and a link from adult growth to spawning participation for this latter life stage. At the same time, the CEM retains direct links from thermal stress to survival and spawning participation because thermal stress can affect these outcomes directly, too, separately from any effects it may have on growth.

Updates to Chapter 4 – Habitat Elements

AQUATIC MACROPHYTES

The definition and discussion of this habitat element are updated as follows:

***Full name*: The taxonomic composition, size range, spatial and temporal distributions, and abundance of the aquatic macrophyte assemblage**. Aquatic macrophytes consist of submerged, emergent, and floating species, including large, plant-like algae. This element refers to the range of aquatic macrophytes that inhabit the shallows of the LCR, its connected backwaters, and isolated wetlands across the LCR flood plain. Table 2 lists the aquatic macrophytes known to occur along the LCR and its backwaters and ponds, following Fernandez and Madsen (2013), Marsh et al. (2013), Mueller (2006, 2007), the National Invasive Species Information Center (NISIC) (2018), Ohmart et al. (1988), and the U.S. Department of Agriculture's (USDA) PLANTS Database (USDA 2018). The species listed in table 2 and the detritus from them may provide cover and food for FLSU; habitat, including periphyton foods, for aquatic and terrestrial invertebrates that FLSU may consume; and habitat for aquatic invertebrates, aquatic vertebrates, and birds that may prey on or compete with FLSU (see chapter 3, "Competition," "Foraging," "Predation," and "Resting/Hiding").

Aquatic macrophytes also reduce turbidity within their stands, by reducing water flow velocities and turbulence, allowing suspended solids to settle to the substrate (Faber-Langendoen et al. 2008; Kadlec and Knight 1996; Mitsch et al. 2005). Prolonged elevated turbidity presumably reciprocally may affect aquatic macrophyte recruitment. On the other hand, extremely high densities of macrophytes presumably also could exclude FLSU, and potentially could limit light penetration to the water surface and water circulation, thereby affecting DO concentrations and possibly other aspects of water chemistry (Finnegan 2013; NISIC 2018). However, LCR MSCP field investigations at the BBCA over the past several years have tracked or captured PIT-tagged FLSU subadults almost exclusively in dense emergent vegetation—predominantly California or giant bulrush and/or softstem bulrush (*S. tabernaemontani*)—during daylight hours, suggesting that at least FLSU subadults have a high tolerance for high macrophyte density (LCR MSCP 2018). Field investigators along the LCR also report difficulties detecting electronically tagged FLSU that enter stands of aquatic macrophytes (LCR MSCP 2018).

Historically, the types, abundance, and distribution of aquatic macrophytes along the LCR and its backwaters depended on the availability of at least relatively stable channel shoreline and off-channel wetland shallows (Johnson 1991;

Ohmart et al. 1988). Aquatic macrophytes in these settings in fact may have helped sustain their own habitat by stabilizing substrates and slowing the movement of water (Carlson et al. 1979; Fernandez and Madsen 2013).

Table 2.—Update of table 4, Aquatic macrophytes of the LCR

Species	Origin[1]
Arundo donax, giant reed	I
Certophyllum demersum, hornswort or coon's tail	N
Chara sp., muskgrass	N
Cladophora glomerata	N
Lemna sp., duckweed	N
Myriophyllum spicatum, Eurasian watermilfoil	I
*Myriophyllum brasiliense (*aka *M. aquaticum)*, parrot feather watermilfoil	I
Najas guadalupensis, southern naiad	N
Najas marina, spiny naiad	N
Nitella sp.	N
Phragmites australis, common reed	?
Potamogeton crispus, curlyleaf pondweed	I
Potamogeton foliosus, leafy or narrowleaf pondweed	N
Potamogeton nodosus, American pondweed	N
Ruppia maritime, widgeongrass	N
Salvinia molesta, giant salvinia	I
Schoenoplectus americanus,[2] three-corner or chairmaker's bulrush	N
Schoenoplectus californicus,[2] California or giant bulrush	N
Schoenoplectus tabernaemontani, softstem bulrush	N
Stuckenia filiformis, fineleaf pondweed	N
*Stuckenia pectinata (*aka *Potamogeton pectinatus)*, sago pondweed	N
Typha angustifolia, narrowleaf cattail	N
Typha domingensis, southern cattail	N
Typha latifolia, broadleaf cattail	N
Typha x glauca, hybrid cattail	?
Utrichularia sp., bladderwort	N
Zannichellia palustris, horned pondweed	N

[1] Key: I = introduced, N = native, and ? = disputed.
[2] Species formerly classified as genus *Scirpus*.

The aquatic macrophyte assemblage along the LCR and its backwaters has changed as a result of river regulation and introductions of non-native plant species. Shallow backwaters, embayments, and tributary confluences continue to support aquatic macrophytes (Fernandez and Madsen 2013). However, river regulation, channel confinement, and flood plain development have greatly reduced the availability of these mesohabitat types. At the same time, the highly invasive giant salvinia (*Salvinia molesta*) is spreading in the LCR ecosystem (NISIC 2018). Fortunately, control efforts appear to be effective (Thorson et al. 2014). One or more possibly non-native varieties of common reed (*Phragmites australis*) (Saltonstall 2002) also may occur, contributing to the spread of common reed throughout the LCR ecosystem.

Hybrid cattails also may affect the LCR macrophyte community. The species, *Typha* x *glauca*, is a hybrid of the native narrowleaf and broadleaf cattail (*T. angustifolia* and *T. latifolia*, respectively) or possibly sometimes a hybrid of broadleaf with the native southern cattail (i.e., with *T. domingensis*) (USDA 2018). Narrowleaf and hybrid cattails have similar habitat requirements and can grow in deeper water compared to broadleaf cattails (Motivans and Apfelbaum 1987). Both narrowleaf and hybrid cattails aggressively out-compete broadleaf and southern cattails for habitat not only by occupying deeper waters but by establishing themselves in dense, monospecific stands. Such stands can quickly dominate entire wetlands, eliminating open water and forming dense rhizome mats and litter, thereby crowding out other plants (Motivans and Apfelbaum 1987). Individual hybrid plants can produce as many as 700,000 fruits per year, and can reproduce asexually from their rhizomes, forming clones that can spread up to 8 meters per year (Pennsylvania Department of Conservation and Natural Resources [PADCNR] 2016). Aggressive expansion is more likely in disturbed wetlands, and hybridization exacerbates this potential. Disturbances that may trigger such aggressive expansion include changes in hydrology, wildfire suppression, or nutrient enrichment (Wilcox et al. 1984), common risk factors across the LCR ecosystem.

The USDA PLANTS Database (USDA 2018) currently does not identify any occurrences of hybrid cattails within the LCR ecosystem. However, this apparent absence may only reflect a pattern of misidentification resulting from the lack of systematic attention to the taxonomy of cattails along the LCR and difficulties in distinguishing between narrowleaf and hybrid cattails in the field (PADCNR 2016). All three parent *Typha* species occur along the LCR, and hybridization occurs easily; therefore, it is likely that hybrid cattails are present along the LCR.

Changes to the aquatic macrophyte assemblage along the LCR involving cattails, common reed, or giant salvinia will have as yet unknown ecological consequences (McFarland et al. 2004; Rogalski and Skelly 2012). For example, overly dense stands of these aquatic macrophytes may suppress aquatic invertebrate abundance by reducing light and DO levels (NISIC 2018) and may provide less cover habitat for larger FLSU. Conversely, different aquatic macrophytes have different ranges of tolerance for variation in water chemistry, including the availability of nutrients. Consequently, any changes in water quality could affect aquatic macrophyte composition and density in some LCR ponds (Finnegan 2013).

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

AQUATIC VERTEBRATES

The definition and discussion of this habitat element are updated as follows:

***Full name*: The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of aquatic vertebrates that may interact with FLSU or its habitat along the LCR**. Interactions may include predation on, competition with, or serving as food items for FLSU. Most of these vertebrates are native and non-native fishes. Activity levels may vary in response to other habitat conditions (e.g., water temperature and water quality).

Table 3, which updates table 5 in the original FLSU conceptual ecological model (Braun 2015a), lists all aquatic vertebrates reported in the present-day LCR (Gloss and Coggins 2005; Marsh and Pacey 2005; Minckley 1991; Minckley et al. 2003; Mueller and Marsh 2002; Nonindigenous Aquatic Species 2017; Ohmart et al. 1988; Pool et al. 2010). Table 3 mostly lists fishes, but also includes the bullfrog (*Rana catesbeiana*), following Mueller (2006, 2007) and Mueller et al. (2006). Table 3 does not include species introduced into the LCR prior to 1975 (e.g., as listed by Miller 1952 and Mueller and Marsh 2002) that do not appear in more recent records, indicating the species likely no longer occur in the LCR. Table 3 includes species that occur in Lake Mead but not species that occur only in its tributaries. The table also includes species found in the Bill Williams River (Shafroth and Beauchamp 2006), but not the Gila River, because FLSU do not have access to the latter but potentially do have access to the former through its confluence with Lake Havasu.

Table 3 indicates 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 2018). Table 3 also indicates which aquatic vertebrate species the literature explicitly reports or proposes in any life stage as a predator on FLSU in both the Lower and Upper Colorado River (see chapter 3, "Predation").

Table 3.—Update of table 5, Aquatic freshwater vertebrates of the LCR

Species	Origin[1]	Prey[2]	Comp$_J$[3]	Comp$_A$[3]
Agosia chrysogaster, longfin dace	N		?	?
Ameiurus melas, black bullhead	S	X	?	?
Ameiurus natalis, yellow bullhead	S	X	?	?
Carassius auratus, goldfish	Other		?	?
Catostomus insignis, Sonora sucker	N		?	?
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		?	?
Tilapia zillii, redbelly tilapia	B		?	?
Xyrauchen texanus, razorback sucker	N	?	?	?

[1] **B** = introduced bait or forage fish, **N** = native, and **S** = introduced sport fish.

[2] Is species known to prey on FLSU?

[3] Do juveniles ($_J$) or adults ($_A$) of the species compete with FLSU for food or habitat?
"X" = reported in LCR literature, "?" = suggested by analogy with BONY or RASU, species data in Froese and Pauly (2018), NatureServe Explorer (NatureServe 2018), or the U.S. Geological Survey's Nonindigenous Aquatic Species Program database (http://nas.er.usgs.gov/default.aspx).

The literature reporting or proposing individual aquatic vertebrate species as a predator on FLSU (or on RASU or BONY, as possible analogs) includes Bezzerides and Bestgen (2002), Brooks et al. (2000), Christopherson et al. (2004), Douglas and Douglas (2000), Johnson et al. (2008), Marsh and Douglas (1997), Miller and Lamarra (2006), Pilger et al. (2008), Rees et al. (2005), Robinson and Childs (2001), Ryden (2000a), Walters et al. (2012), Ward (2001), Ward et al. (2002), and Yard et al. (2011). Predation by RASU, BONY, and common carp (*Cyprinus carpio*) on FLSU eggs is suspected by analogy, with evidence of all three species preying on BONY eggs and BONY preying on RASU eggs (Bozek et al. 1984; Mueller 2006). Predation by bullfrogs on small FLSU is assumed based on bullfrog feeding ecology and by analogy with evidence of bullfrogs preying on small RASU (Mueller et al. 2006).

Finally, table 3 indicates which other aquatic vertebrates have ecological characteristics suggesting they could prey on FLSU and also indicates which aquatic vertebrates have ecological characteristics suggesting their juveniles or adults could compete with FLSU for food items or physical habitat. The latter information on ecological characteristics comes from the FishBase (Froese and Pauly 2018) and NatureServe Explorer (NatureServe 2018) databases.

The large number of entries in table 3 for possible competition reflects the fact that FLSU are omnivorous (see chapter 3, “Foraging”). 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.

BIRDS AND MAMMALS

The definition and discussion of this habitat element are updated as follows:

***Full name*: The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the bird and mammal assemblages**. This element refers to the range of bird and mammal species known or suspected to interact with FLSU or its habitat along the LCR and its connected backwaters. This range includes species known or potentially able to prey on FLSU specifically when the fish occur in shallows or approach the water surface or shoreline, making the fish visible and accessible.

Investigators in recent years have expanded the list of bird species known or suspected to prey on native fishes along the LCR. The list now includes great blue herons, kingfishers (*Megaceryle alcyon*), osprey, American white pelicans (*Pelecanus erythrorhynchos*), possibly other *Pelecanus* spp., and double-crested cormorants (and possibly other cormorants such as the neotropical cormorant, [*Phalacrocorax brasilianus*]) (Best 2015; Best et al. 2017; Humphrey et al. 2014, 2015, 2016; Kesner et al. 2008; Lantow 2017; LCR MSCP 2017; McCall et al. 2017; Mueller 2006, 2017). Humphrey et al. (2016) also report turkey vultures (*Cathartes aura*) roosting in the vicinity of FLSU habitat in the Bill Williams River National Wildlife Refuge. Best et al. (2017) also report the following other species visiting or roosting at Laughlin Lagoon during periods when FLSU and other native fishes were present: Cooper's hawks (*Accipiter cooperii*), western grebes (*Aechmophorus occidentalis*), golden eagles (*Aquila chrysaetos*), great egrets (*Ardea alba*), American bitterns (*Botaurus lentiginosus*), northern harriers (*Circus cyaneus*), snowy egrets (*Egretta thula*), gulls (mostly *Larus delawarensis* but possibly also *L. californicus*), common mergansers (*Mergus merganser*), and black-crowned night herons (*Nycticorax nycticorax*).

Knowledge about the ecology of avian predation on native fishes along the LCR has increased particularly through the work of Best et al. (2017) and Mueller (2017) at Laughlin Lagoon and the LCR MSCP at the IPCA. As noted above (see chapter 3, "Predation"), this work has focused on stocked PIT-tagged BONY (see also Lantow 2017; LCR MSCP 2017). Laughlin Lagoon is an artificial backwater connected to the big bend of the Colorado River south of Laughlin, Nevada, opposite Bullhead City, Arizona. The study during winter 2015, spring 2016, and winter 2016 combined the use of photographic arrays on perching/roosting poles with the use of antenna arrays to detect PIT tags from tagged RASU and BONY consumed by birds at the poles. The RASU and BONY were deliberately stocked into the lagoon for purposes of the study. The results indicated significant predation on both fish species by double-crested cormorants, with additional but much lower rates of predation by great blue herons and osprey. Further, the birds consumed BONY and RASU regardless of fish size, up to the largest fishes stocked into the lagoon for the study: the mean size of stocked BONY was approximately 312 mm TL while the mean size of depredated BONY was approximately 307 mm TL) (Best et al. 2017).

Lantow (2017) does not provide size data on the BONY stocked or depredated at the IPCA in 2017. However, Lantow (2018) notes that LCR MSCP biologists observed only two cormorants total on the IPCA ponds for the first 6 months following stocking of BONY in 2017 but after 12 months now observe more cormorant activity. This activity typically consists of two to four birds feeding primarily in Pond 2, where a large spawn of BONY occurred in 2017, resulting in "lots of small fish in the pond" (J. Lantow 2017, personal communication). LCR MSCP biologists also observed great blue herons in the area prior to the BONY stocking, "presumably feeding on mosquitofish in the drainage ditch or Pond 5" (J. Lantow 2017, personal communication), but observed them at all ponds occasionally following the stocking. The stocking of BONY at the IPCA in 2017 thus may have resulted in a greater abundance and/or higher activity level of avian predators at the site.

Much literature exists on the ecology and management of avian piscivory (e.g., Beckmann et al. 2006; Cezilly 1992; Cowx 2003; Steinmetz et al. 2003;

Wiese et al. 2008). Much of this literature concerns commercial fisheries and aquaculture. However, this literature presents information potentially relevant to the problems posed by avian piscivory on native fishes of the Colorado River Basin. Cezilly (1992), for example, examines the idea of using turbidity as a tool to control rates of avian piscivory. This CEM update does not attempt to review the literature on the ecology and management of avian piscivory either in general or with respect to the use of turbidity or dyes of different colors to reduce the ability of avian predators to see potential prey in the water. The LCR MSCP did experiment informally in 2016 with using an aquaculture dye to suppress algal and aquatic macrophyte production in an off-channel pond used for rearing RASU, recognizing that the dye might also affect avian predation. Double-crested cormorants and great blue herons have been observed at this and other off-channel rearing ponds, notably in the winter months immediately following stocking. Unfortunately, a storm breached the berm separating the pond from Lake Mohave, ending the experiment prematurely after only 2 months (Loomis 2018, personal communication). The experiment did not include systematic observations of avian predation.

Information on mammalian predation on FLSU or any other native fish species along the LCR has not expanded since the completion of the original FLSU conceptual ecological model. The main source of information on this topic remains Mueller (2006), which reports observations of and reasons for suspecting mammalian predation on RASU at Cibola High Levee Pond by "… raccoons [*Procyon lotor*], ringtail cats (*Bassariscus astutus*), and other fish-eating animals." Mueller (2006) also suggests that coyotes (*Canis latrans*) could prey on fishes when they approach the shoreline, an instance of which Montony (2010) subsequently caught on camera at the IPCA. LCR MSCP investigators in 2014 also observed coyotes appearing to forage along the shallow shoreline at Davis Cove, an off-channel backwater of Lake Mohave, after a large BONY spawn. However, the investigators did not photograph or video record the event (Loomis 2018, personal communication). FLSU do not occur at either Cibola High Levee Pond or the IPCA, but the predation of RASU by mammals at these sites suggests that these same mammal species could as easily prey on FLSU where they do occur.

This update also recognizes that at least two mammals may affect FLSU along the LCR not through predation but by shaping habitat. Specifically, beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*) were once common in the LCR ecosystem and once helped shape mesohabitat conditions by introducing woody debris and creating marshes and pools along backwater channels (Grinnell 1914; Hautzinger 2010; Kniffen 1932; Minckley and Rinne 1985; Ohmart et al. 1988; Stevens et al. 1997; Yohe, II 1998). Both species are still present (Boutwell 2002; Kesner et al. 2008; Montony 2010; Mueller 2006, 2007; Mueller et al. 2005, 2008; Shafroth and Beauchamp 2006). Both mammals also eat aquatic macrophytes and thereby may both shape macrophyte availability and generate POM at the same time (Henker 2009), potentially affecting food availability and physical habitat for FLSU.

As with predation on FLSU by other aquatic vertebrates, the intensity, timing, and geographic distribution of predation on FLSU by birds and mammals depends on more than simply the presence and abundance of the potential predators. Other habitat elements that may also affect activities of potential avian and mammalian predators include the season and time of day, air temperature and other weather conditions, wave activity, turbidity, and the availability of perch (Best et al. 2017; Mueller 2006) or cover habitat for the predators.

FLSU vulnerability to avian and mammalian predation, further, may also depend on turbidity and the availability of vegetative cover (see "Aquatic Macrophytes" and "Turbidity," this chapter). Other factors that may affect FLSU vulnerability to avian and mammalian predation include FLSU long-distance movements and seasonal movement to spawning sites.

As also noted above (see chapter 3, "Predation"), FLSU likely evolved under ecological and evolutionary pressure from avian predation. FLSU behaviors in natural settings, such as movement to greater depths during daylight and use of living and dead vegetation as cover in shallow waters (see chapter 3, "Predation," and "Aquatic Macrophytes," this chapter), could have evolved at least partially in response to such pressure, as may some aspects of FLSU morphology and swimming behaviors (see chapter 3, "Predation"). The FLSU living in the LCR also are survivors in a predator-rich environment and therefore likely exhibit a more complete range of avoidance behaviors than may RASU or BONY reared in hatcheries and grow-out ponds before release into this same environment.

FISHING ENCOUNTERS

No change.

FLOW NETWORK FRAGMENTATION

No change.

GENETIC DIVERSITY

This is a new habitat element in the CEM, defined as follows:

***Full name*: The genetic diversity of FLSU individuals**. This element refers to the genetic homogeneity versus heterogeneity of the FLSU population during each life stage. The genetic diversity of FLSU in the LCR ecosystem is affected by two factors: (1) potential hybridization of FLSU with RASU and (2) potential isolation of the FLSU population between Davis Dam and Lake Havasu, the only population of FLSU in the LCR ecosystem. The greater the genetic diversity of a population, the greater the possibility that individuals of a given life stage will have genetically encoded abilities to survive their encounters with the diverse stressors presented by their environment and/or take advantage of the opportunities presented by their environment (LCR MSCP 2006, 2016, 2017; Minckley et al. 2003; Osborne and Turner 2014, 2015, 2016, 2017; USFWS 2002). As discussed in chapter 3 (see "Hybridization"), hybridization can also contribute to genetic diversity and consequently to species resilience in the face of new stressors or opportunities. Conversely, a population with a very limited gene pool may have less resilience in the face of new stressors or opportunities and greater vulnerability to extirpation.

As noted elsewhere in this CEM (see chapter 3, "Hybridization"), FLSU across the Colorado River Basin overall occasionally hybridize with other catostomids, including native RASU and bluehead suckers, and non-native white suckers. Neither bluehead suckers nor white suckers occur within the LCR (Bezzerides and Bestgen 2002; Fuller 2018). However, recent data from Lake Mead and the Grand Canyon, where both FLSU and RASU occur and have successfully produced new cohorts, demonstrate that FLSU readily hybridize with RASU. Fish surveyors, over the course of the present decade, have repeatedly captured FLSU-RASU hybrids in both waterbodies (Albrecht et al. 2010a, 2010b; BIO-WEST, Inc., and American Southwest Ichthyological Researchers 2017; Dowling et al. 2014a, 2014b, 2015, 2016; Gilbert et al. 2017; Kegerries and Albrecht 2011, 2013; Kegerries et al. 2016, 2017; Mohn et al. 2016; Reclamation 2017, 2018; USFWS 2016; Wolters et al. 2016, 2017). Genetic data indicate past hybridization between the two species, affecting the genetic makeup of the present RASU population in Lake Mohave, as well (Marsh et al. 2015). The present reviewer did not locate any reports of FLSU-RASU hybrids between Davis Dam and Lake Havasu, the only portion of the LCR where FLSU are present—a section of the river where RASU also are stocked (Marsh et al. 2015; LCR MSCP 2017, 2018). However, the literature also does not indicate whether monitoring for such hybrids along this section of the river has been a priority.

The FLSU between Davis Dam and Lake Havasu genetically descend from individuals released below the dam by the Arizona Game and Fish Department (AGFD) in 1976 to help control black flies in this section of the river (Mueller and Wydoski 2004). The FLSU released in 1976 were captured by the AGFD at the Paria River – Colorado River confluence at Lees Ferry, above the Grand Canyon. Davis Dam prevents fish movement up or downstream, and no FLSU occur in Lake Havasu. However, the LCR MSCP has introduced additional FLSU into this section of the river since 2014. These additional individuals were captured originally in the Colorado River inflow arm of Lake Mead and reared to subadult to adult size at the Lake Mead Fish Hatchery (a Nevada State facility) for use in research (e.g., LCR MSCP 2018). The LCR MSCP has released 20–42 of these reared FLSU annually into Laughlin Lagoon since 2014, after insertion of either PIT or sonic tags, for telemetric monitoring (e.g., LCR MSCP 2018). These introduced FLSU potentially have also contributed to the genetic diversity of the FLSU population below Davis Dam, preventing the genetic isolation of this population from the FLSU of Lake Mead.

INFECTIOUS AGENTS

No change.

INVERTEBRATES AND PARTICULATE ORGANIC MATTER

No change.

MACROHABITAT STRUCTURE

This habitat element replaces the original habitat element, “Macrohabitat Geometry,” with an updated definition and discussion as follows:

***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 and hydraulic gradient of the river channel, backwaters, other off-channel wetted areas, and the connected flood plain. The present CEM distinguishes macrohabitats from mesohabitats, which are smaller-scale features such as eddies, pools, riffles, and runs (see below, this chapter). Some authors alternatively refer to both larger- and smaller-scale features as macrohabitat types (e.g., Budy et al. 2009; Holden 1999) (see also “Mesohabitat Structure,” this chapter). Examples of macrohabitat types, as defined in the FLSU conceptual ecological model, include the main channel, islands, side channels, tributary mouths, sloughs, bays, connected and disconnected backwaters, delta lagoons, etc. Major artificial features of the LCR, such as channel training structures, diversion and return structures, and dams (LCR MSCP 2004) also constitute macrohabitats for purposes of this model.

Macrohabitats define the overall flow paths and gradients for water and sediment moving through the system and establish the template for the formation of mesohabitats. Macrohabitat structure along the LCR historically was shaped by main stem and tributary riverflows and also by their sediment transport, interacting with surficial geology and flood plain vegetation. The historic macrohabitat structure of the LCR remains only in a few places where the channel is confined by bedrock and at a few unaltered tributary confluences (Mueller and Marsh 2002). Otherwise, the macrohabitat structure along the LCR today depends more on the design and operation of the main stem water storage-delivery system, tributary inflow, and flood plain, channel, and shoreline management. All of these factors apply to the single section of the LCR currently occupied by FLSU between Davis Dam and Lake Havasu.

Literature reviews and more recent studies (e.g., Bezzerides and Bestgen 2002; Budy and Salant 2011; Budy et al. 2009; Cathcart 2014; Franssen et al. 2014; Laub and Budy 2015; Rees et al. 2005; Walters et al. 2012) indicate that older juvenile to adult FLSU are macrohabitat generalists. They occur in a wide range of natural macrohabitats, including both confined (i.e., canyon) and unconfined channels of large rivers and streams, both braided and non-braided reaches along these channels, and backwaters at river confluences, particularly during main stem high flow pulses. However, they occur only infrequently in small headwater streams. Spawning occurs along larger tributaries and the main stem Colorado River at locations that appear to be determined by mesohabitat and finer-scale conditions rather than macrohabitat type. Fry and early juveniles use a more limited range of natural macrohabitat types, including backwaters and shoreline pools along rivers.

Major artificial features of the LCR, such as channel training and shoreline stabilization structures, diversion and return structures, and dams, also constitute macrohabitats for purposes of this model (LCR MSCP 2004). FLSU avoid tailwater zones below dams, although this may be due to the significantly colder temperatures found in these zones (see also Bezzerides and Bestgen 2002; Rees et al. 2005). FLSU fry and early juveniles may be found in reservoirs, where they may find suitable nursery habitat near confluences. Otherwise, as discussed above, adult FLSU throughout the Colorado River Basin in the past have mostly avoided or failed to persist in lotic environments such as reservoirs. However, as also noted above in this update, recent evidence from Lake Mead demonstrates FLSU movement within the lake through open, lentic conditions over distances of 10–50 km. The literature does not yet provide evidence or suggestions for the conditions that have favored such movements within Lake Mead, in contrast to the pattern of avoidance observed previously throughout the rest of the Colorado River Basin.

MESOHABITAT STRUCTURE

This habitat element replaces the original habitat element, “Mesohabitat Geometry/Cover,” with a slightly updated definition as follows:

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

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

Examples of mesohabitat types in the LCR ecosystem include bars, eddies, nearshore slackwaters, littoral and deltaic shallows, aquatic macrophyte stands, pools, islands, point-bars, riffles, and runs. Some authors alternatively refer to such features as macrohabitat types (e.g., Budy et al. 2009; Holden 1999) (see also "Macrohabitat Structure," this chapter). Mesohabitats may include features such as aquatic macrophyte patches, large woody debris, overhangs, and interstitial spaces and hollows in banks and substrates that can provide resting/hiding habitat for FLSU of different life stages. As noted in chapter 3 (see "Drifting"), 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 distinct type of mesohabitat. This document suggests calling such settings "interception habitat," following terminology developed for a CEM to support recovery of the endangered pallid sturgeon along the Missouri River (Jacobson et al. 2016). However, the literature on mesohabitats and native fish ecology along the Colorado River does not yet use this term.

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

The mesohabitat structure along the LCR historically was shaped by the same factors that shaped macrohabitat structure, but at finer spatial scales, such as by main stem and tributary riverflows and their loads of sediment and large woody debris interacting with flood plain vegetation and geology. The sizes and distribution of large woody debris historically also affected the types, distribution, and stability of mesohabitats along the LCR (Minckley and Rinne 1985; Mueller and Marsh 2002; Utah Department of Natural Resources [UDWR] 2009). Stranded large woody debris diverts the flow of water and transports sediment, creating localized suites of mesohabitats, including eddies, pools, and bars, and also creates overhangs and pockets of shade.

Mesohabitat structure similar to historic conditions presently occurs only in a few places where the channel is confined by bedrock and at tributary confluences. Otherwise, today, mesohabitat structure depends on main stem water storage-delivery system design and operations, tributary inflows, channel and shoreline engineering, and the effects of macrohabitat structure. Dams have eliminated almost all inputs of sediment and large woody debris (Minckley and Rinne 1985) from the upper to the LCR and from one LCR reach to the next. However, remnants of individual historic mesohabitat sites persist (LCR MSCP 2016; Minckley et al. 1991; USFWS 2002).

Table 4 updates table 6 in the original FLSU conceptual ecological model (Braun 2015a). As with the original table, table 4 summarizes published information on the mesohabitat types in which FLSU in different life stages have been observed (Best and Lantow 2010, 2011, 2012a, 2012b, 2015; Beyers et al. 2001; Bezzerides and Bestgen 2002 and references therein; Budy and Salant 2011 and references therein; Douglas and Douglas 2000; Farrington et al. 2013; Hoffnagle 2000; Holden 1999 and references therein; Joseph et al. 1977 and references therein; Kegerries et al. 2016; LCR MSCP 2005, 2016 and references therein, 2018; McIvor and Thieme 1999; Minckley and Marsh 2009; Muth and Nesler 1993; Rees et al. 2005 and references therein; Robinson et al. 1998; Thieme 1997; Thieme et al. 2001; Valdez et al. 2001).

The mesohabitat types listed in table 4 are not mutually exclusive. For example, stands of emergent vegetation can occur in geomorphic settings such as backwaters, shorelines, side channels, and slackwater sites, and pools and areas of slackwater can both occur along shorelines. The areas of a backwater with, versus without, aquatic macrophytes would present FLSU with different mesohabitat conditions.

The findings in table 4—as with table 6 in the original FLSU conceptual ecological model—come with an important caveat: No single classification exists for mesohabitat types along the LCR or in the UCRB in general. Holden (1999) and Stewart and Anderson (2007) (see also Stewart et al. 2005) present detailed classifications, but other studies use mesohabitat terms less formally. Different

Table 4.—Update of table 6, FLSU mesohabitat associations by life stage

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

investigators may also use different terms to refer to essentially the same mesohabitat type, and terms may vary between the LCR and UCRB (LCR MSCP 2005). For example, Hoffnagle (2000) describes “backwaters” along the Grand Canyon as “… pockets of water partially isolated from the main channel by a sand bar [that] usually form immediately downstream from a channel constriction, such as a debris fan.” In contrast, Best and Lantow (2012a, 2012b) appear to classify such settings along the LCR below Davis Dam as shoreline slackwaters, shoreline pool habitats, or backwaters, all of which potentially could also be classified as types of interception habitat for drifting larvae (see also Kegerries et al. 2016).

Most studies report that FLSU may occur in almost any mesohabitat, although potentially only as transients. The most common associations reported (greatest proportions of observations within individual studies) for FLSU life stages with specific mesohabitat types are adults with pools and runs; both subadults and adults with aquatic macrophytes, particularly California and softstem bulrush; fry and early juveniles with backwaters (including secondary channels), slackwaters, and shoreline mesohabitats; and spawning adults with gravel or cobble bars (also sometimes termed "shoals") at confluences and below riffles and pools. Studies have also reported that FLSU occur more abundantly along river reaches with greater channel complexity (i.e., with a greater diversity of mesohabitats in close proximity) (Franssen et al. 2014; LCR MSCP 2005; Zelasko et al. 2011).

FLSU also reportedly seek mesohabitats with overhead cover. Cross (1975, cited in LCR MSCP 2005) reports that more than 50% of FLSU capture locations along the Virgin River included boulders, overhanging trees, or undercut banks. The LCR MSCP tracking of PIT-tagged FLSU adults and subadults, between Davis Dam and Lake Havasu, repeatedly found that the tagged FLSU mostly concealed themselves in bulrush stands during daylight hours but moved into open waters at night (Best and Lantow 2010, 2011, 2012a, 2012b, 2015; LCR MSCP 2018). This same monitoring effort also found that FLSU subadults and adults remained in open waters in backwater settings when turbidity was high, even when aquatic macrophyte cover also was available (LCR MSCP 2018).

As noted in the original FLSU conceptual ecological model (Braun 2015a), many reports of FLSU mesohabitat associations qualify their labels for mesohabitat types with information on depth and flow velocity (e.g., "moderate to deep" pools, "shallow" riffles) (Anderson and Stewart 2007; Budy and Salant 2011; Kegerries et al. 2016), or "nearshore low-velocity" habitats (Robinson et al. 1998), or they use alternative terms for the same settings, such as near-shore slackwater and nearshore low-velocity habitat. Where available, quantitative information on water depths, flow velocities, substrate size, and aquatic vegetation permit a refined qualification of mesohabitat conditions as discussed below (see "Substrate Texture/Dynamics," "Water Depth," and "Water Flow, Turbulence," this chapter). FLSU use of different mesohabitats may vary with other conditions such as water temperature and turbidity (LCR MSCP 2018; Minckley and Marsh 2009).

MONITORING, CAPTURE, HANDLING

This habitat element replaces the original habitat element, "Scientific Study," with a slightly updated definition as follows:

***Full name*: The types, frequencies, and duration of scientific monitoring, capture, and handling of FLSU**. This element refers to the possible capture, examination, tagging, removal, and experimental treatment of FLSU in the LCR ecosystem. This element does not refer to the scientific study of FLSU at hatcheries or rearing facilities. Field and laboratory investigations always follow standard procedures during capture and handling to minimize stress (Ward 2006). Detection and capture methods and their associated sampling designs may vary in their suitability for different mesohabitats, in their likelihood of encountering

FLSU of different sizes and life stages, and in their effects on captured individuals (Bestgen et al. 2007a, 2007b; Karp and Tyus 1990; LCR MSCP 2018; Ward 2006).

The original FLSU conceptual ecological model (Braun 2015a) noted a paucity of literature on the possible impacts of scientific study on FLSU compared to a large body of literature documenting the impacts of scientific study on RASU and BONY. Chart and Bergersen (1992) notes that handling may have caused stress to FLSU that resulted in their passive drift downstream following release. Ward (2001) notes that repeated handling of FLSU during laboratory studies may have slowed their growth. This update expands on this modest information. Fraser et al. (2017), during their study of FLSU movement between rivers and tributaries, found that FLSU scattered and moved downstream out of the subject tributaries within a few hours after capture in fyke nets and handling. In contrast, FLSU previously implanted with PIT tags and tracked using only remote PIT tag antenna arrays remained in the same tributaries for 10–12 days.

The LCR MSCP (2018) also has noted a relationship between FLSU behavior and detection during monitoring. As noted above, telemetric monitoring of sonic-tagged FLSU released below Davis Dam found that detection of FLSUs was noticeably more difficult when they moved into the cover of bulrush stands during the daylight hours. Presumably, the monitoring teams could not move their ultrasonic receivers into these stands of emergent vegetation, and the fish moved far enough into the vegetation to escape the detection radius of the receivers. Aquatic macrophyte vegetation also attenuates sonic tag signals (Lantow 2018, personal communication). More generally, this update hypothesizes that FLSU resting/hiding and swimming behaviors potentially may affect the likelihood of FLSU detection and capture by different methods (see chapter 3, "Resting/Hiding" and "Swimming").

SUBSTRATE TEXTURE/DYNAMICS

No change.

TURBIDITY

The definition of this habitat element has been updated as follows:

***Full name*: The magnitude and spatial and temporal distributions of turbidity**. This element refers to the turbidity at sites potentially used by FLSU in each life stage and its pattern of variation over time and among macro- and mesohabitat settings. The Colorado River prior to its regulation was highly turbid, especially along its main channel and during high-flow pulses, with lower turbidity along channel margins and in off-channel settings (Minckley 1991; NRC 1991; Ohmart et al. 1988). The sources of this turbidity included inputs of suspended matter from tributary watersheds, erosion and deposition along the river during high-flow events, the suspension of POM by vertical and horizontal currents in the river and its backwaters during lower flow conditions, and phytoplankton production. FLSU also occupied—and still occupy—headwater streams with naturally lower turbidity than that found along larger rivers in the Colorado River basin (Dauwalter et al. 2011a, 2011b; Sweet et al. 2009). FLSU evolved in this environment, and turbidity therefore presumably affects—both directly and indirectly—several aspects of FLSU ecology.

River regulation has drastically altered the turbidity regime—the spatial distribution, magnitude, timing, and persistence of turbidity—along the main stem LCR, trapping most of the river's natural sediment load in impoundments and preventing erosive high-flow events (NRC 1991). Turbidity levels rise only along river sections with relatively high-energy managed flows, such as along the Colorado River in the Havasu National Wildlife Refuge above Lake Havasu, or more locally from channel and shoreline engineering activities (LCR MSCP 2004). Turbidity in impoundments can vary as a result of changes in lake levels, which can expose formerly submerged fine sediments, particularly in deltaic mesohabitats, where the exposed sediments are subject to "erosion and suspension by river currents and wave action, resulting in increased turbidity levels at the inflow" (Valdez et al. 2012). The turbidity regime in connected backwaters—for example, in Laughlin Lagoon, the BBCA, or Topock Marsh—mostly depends on inputs from the river, suspension by turbulence driven by the wind and localized currents within the backwaters, and disturbances of banks and substrates by human activities. The turbidity regime in isolated ponds along the LCR mostly depends on suspension by turbulence driven by the wind and internal (e.g., thermal) currents, and disturbances of banks and substrates by human activities.

Biological dynamics also affect turbidity in all these settings. Phytoplankton production can rise to a level where it affects turbidity. Bioturbation of benthic sediments, such as by common carp during feeding and spawning (Cucherousset and Olden; 2011Rogers et al. 2008) or by mayfly larvae (Osterling et al. 2007), also may cause localized increases in turbidity for the duration of the disturbance. Nuisance species may also affect turbidity as a result of algal blooms or, conversely, when non-native quagga mussels (*Dreissena bugensis*) and zebra mussels (*Dreissena polymorpha*) filter out large amounts of plankton and POM. Finally, as noted earlier (see "Aquatic Macrophytes," this chapter), aquatic macrophyte stands reduce turbidity by reducing water flow velocities and turbulence, allowing suspended solids to settle to the substrate (Faber-Langendoen et al. 2008; Kadlec and Knight 1996; Mitsch et al. 2005).

Reports on FLSU ecology document the following direct effects—or lack of effects—of varying turbidity. As noted in the original FLSU conceptual ecological model (Braun 2015a), different studies use different methods and measurement units to assess turbidity. The following discussion therefore must use relative terms to describe levels of turbidity:

- High turbidity may provide cover for fry, juvenile, subadult, and adult FLSU from predators. As noted above, FLSU subadults and adults tracked along the river section between Davis Dam and Lake Havasu using PIT tags remained in open water when turbidity levels were high but moved into or remained in aquatic macrophyte stands when turbidity levels were low (Best and Lantow 2010, 2011, 2012a, 2012b, 2015; LCR MSCP 2018). These observations are consistent with reports by the AGFD (1996; cited in Hoffnagle 2001) of increased catches of FLSU under turbid conditions (> 30 nephelometric turbidity units). The AGFD findings suggest that, under turbid conditions, FLSU may move into open water settings where they consequently also become more susceptible to capture in nets (see Clark et al. 2010 for an overview of AGFD field methods). (The fact that the same pattern of FLSU movement into turbid waters is apparent in both telemetric and net-capture studies indicates that the elevated net-capture results are not simply due to a reduced ability of FLSU to detect nets under turbid conditions). FLSU thus appear to use high turbidity and aquatic macrophyte stands as alternative forms of protective cover (see "Aquatic Macrophytes" and Mesohabitat Structure," this chapter). Of course, the dominant native predatory fish in the LCR, the Colorado pikeminnow (see chapter 3, "Predation"), evolved in the same turbid ecosystem, and turbidity does not limit its foraging ability (Muth et al. 2000). Consequently, it is not surprising that FLSU exhibit other behaviors for avoiding predation than simply seeking turbid environments.

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

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

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

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

More generally, Vaage et al. (2015; see also Ward et al. 2016) found that elevated turbidity protected Colorado River native fishes—specifically BONY, RASU, and humpback chub, with which FLSU share many ecological characteristics—from depredation by most non-native fishes more than vegetative cover such as aquatic macrophytes and flooded terrestrial vegetation, and rocky substrates with crevices, at turbidity levels as low as approximately 5% of the median value (in Formazin Turbidity Units) observed in the Colorado River at Lees Ferry prior to river regulation. However, depredation by flathead catfish (*Pylodictis olivaris*), unlike depredation by other non-native fishes, was relatively unaffected by turbidity (Vaage et al. 2015). Humphrey et al. (2016) also note that flathead catfish prefer habitats with higher turbidity and/or similar cover. On the other hand, turbidity has well-known inhibiting effects on avian piscivory in freshwater ecosystems in general (Cezilly 1992).

Reports on FLSU ecology also document the following indirect effects of varying turbidity. Again, as noted in the original FLSU conceptual ecological model (Braun 2015a), different studies use different methods and measurement units to assess turbidity. The following discussion therefore must use relative terms to describe levels of turbidity:

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

- High levels of turbidity may inhibit the abundance of non-native fish species. Clark et al. (2010) suggest that turbidity along the lower Little Colorado River inhibits colonization by non-native fishes. On the other hand, moderately elevated levels of turbidity in the Grand Canyon did not deter non-native rainbow trout (*Oncorhynchus mykiss*) piscivory on FLSU (Yard et al. 2011). The study authors suggest that rainbow trout simply moved to shallow channel margins where their sight-feeding would not be limited and where FLSU also move under the same conditions. However, extreme floods, with associated extreme turbidity, displaced and/or resulted in direct mortality of rainbow trout along the same river reaches (Coggins and Yard 2010; Coggins et al. 2011). Similarly, Bestgen et al. (2006, 2007b) found that pulses of extreme flow and turbidity along the Green River caused much greater displacement and mortality among smallmouth bass (*Micropterus dolomieui*) than among FLSU. However, smallmouth bass readily tolerate moderate turbidity (Bestgen et al. 2011). As noted above, depredation by flathead catfish appears to be relatively unaffected by turbidity (Vaage et al. 2015), and flatheads may actually prefer habitats with higher turbidity and/or similar cover (Humphrey et al. 2016).

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

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

Finally, turbidity also affects monitoring, capture, and handling. Investigators have long recognized that elevated levels of turbidity have two types of effects on fish monitoring: (1) they limit detection and capture of FLSU by monitoring methods that require visual contact, including recovery of individuals stunned by electroshocking; and (2) they attenuate transponder signals (recently Bestgen et al. 2007a; Rogers et al. 2008; Stone 2010; Van Haverbeke et al. 2013). These circumstances are thought to have resulted in under-detection of FLSU in surveys carried out during high-turbidity events. On the other hand, as noted above, high turbidity may cause or allow FLSU to move from covering habitats out into open water, where they may be more easily captured in nets and, if PIT tagged, tracked using antenna arrays.

WATER CHEMISTRY

The definition of this habitat element has been updated as follows:

***Full name*: The magnitudes and horizontal, vertical, and temporal distributions of water chemistry properties that affect FLSU**. This element refers to the water chemistry at sites potentially used by FLSU in each life stage, including the way that water chemistry may vary over time and space. The element covers parameters such as DO, pH, salinity, naturally occurring dissolved substances, and contaminants such as added nitrate/nitrite, perchlorate, selenium, other metals, and artificial organic compounds (Hinck et al. 2007, 2009; LCR MSCP 2004, 2018; Ohmart et al. 1988; Patiño et al. 2012; Reclamation 2010, 2011a, 2011b; Seiler et al. 2003; Stolberg 2009, 2012; Turner et al. 2011). Contaminants in the LCR, in settings where FLSU occur, arrive from both point and non-point sources (see “Chapter 5 – Controlling Factors” in the original FLSU conceptual ecological model). Water storage-delivery system design and operations (see chapter 5 in the original FLSU conceptual ecological model) also affect water chemistry along the LCR in settings where FLSU occur, including salinity and DO concentrations, through their effects on reservoir operations and releases, and diversions and flow management for off-channel wetlands. Numerous habitat elements affect water chemistry at any given location, particularly water depth, temperature, circulation, and their variation over time.

FLSU during different life stages are suspected to be vulnerable to direct effects from altered water chemistry (Bestgen et al. 2011; Carman 2007; Gido et al. 1997), as would be expected for any fish species. FLSU may directly encounter harmful conditions in the water column, or they may consume contaminants that have bioaccumulated in invertebrates on which they feed. However, little information exists on direct impacts to FLSU from changes in any specific water quality properties, prompting calls for increased monitoring to look for such possible impacts (Rees et al. 2005; UDWR 2009). The ways in which variation in water chemistry may affect FLSU is not a topic of ongoing research among

LCR MSCP work tasks (LCR MSCP 2018). However, the LCR MSCP continues to monitor selenium in backwaters, including the BBCA in the section of the LCR in which FLSU occur (LCR MSCP 2018).

Alterations to water chemistry along the LCR, specifically nutrient enrichment, also affect planktonic and benthic primary productivity (Melis et al. 2010; NRC 1991; Ohmart et al. 1988), which in turn affect turbidity. However, productivity along the LCR may be more limited by the availability of phosphorus than that of nitrogen (Turner et al. 2011). As noted above (see “Invertebrates and Particulate Organic Matter,” this chapter), the LCR MSCP has experimented with fertilizing off-channel habitats around the margins of Lake Mohave using both dissolved nutrients and POM. These experiments were conducted in order to determine if such mechanical fertilization stimulates primary and/or secondary productivity (Loomis 2014). The results have been ambiguous, affected by high variability among test sites and within individual test sites over time, and impacts of poor water circulation, DO depletion during hot weather, and algal mat formation. The LCR MSCP work plan (LCR MSCP 2018) does not include plans for such experiments along the section of the LCR in which FLSU occur, between Davis Dam and Lake Havasu. As also noted above concerning invertebrates along the LCR (see “Invertebrates and Particulate Organic Matter,” in Braun [2015a], chapter 4), toxins released by golden alga blooms could also harm native fishes in backwaters and other waterbodies with limited water circulation.

Pheromones and other olfactory cues in the water could provide FLSU with much-needed information about their environment, as is generally the case with fishes. However, the literature reviewed for this update or for the original FLSU conceptual ecological model did not provide any information on this topic.

WATER DEPTH

No change.

WATER FLOW, TURBULENCE

The discussion of this habitat element has been updated as follows:

As discussed in chapter 2, new information since completion of the original FLSU conceptual ecological model (Braun 2015a) reinforces the understanding that flow conditions play little role in triggering FLSU spawning. This new information comes from three sources. The most significant information comes from the evidence for *in situ* spawning of FLSU in the Colorado River inflow area, Echo Bay, and the Virgin River/Muddy River inflow area of Lake Mead

(Kegerries et al. 2016, 2017; Mohn et al. 2016). These three areas are subject to strongly lake-influenced hydrologic regimes, indicating that FLSU spawning does not depend on the occurrence of specific riverine discharge conditions. Further, Klein et al. (2017) examined statistical relationships of FLSU growth and recruitment to multiple indicators of the hydrologic regime (flow regime) along the upper Green, lower Green, Strawberry, and White Rivers, Utah, in the UCRB. Their results showed that none of the hydrologic indicators or combinations of these indicators reliably predicted variation in FLSU growth or recruitment. Finally, evidence presented by Fraser et al. (2017) strengthens the case for changes in water temperature rather than changes in flow as the most important spawning cue for FLSU (see discussion of water temperature, below).

WATER TEMPERATURE

The discussion of this habitat element has been updated as follows:

As discussed in chapter 2, new information since completion of the original FLSU conceptual ecological model (Braun 2015a) reinforces the understanding that changes in water temperature are the dominant trigger for FLSU spawning. Specifically, Fraser et al. (2017) present evidence that changes in water temperature cue the movement of FLSU into tributaries to spawn in the UCRB. The original FLSU conceptual ecological model also noted that the spawning of FLSU between Davis Dam and Lake Havasu (Best and Lantow 2012a, 2012b) does not contradict the identification of thermal change as the dominant spawning trigger: This section of the river does experience a modified thermal regime. However, the temperature of the air strongly affects the temperature of the water, resulting in relatively natural annual and diurnal patterns of temperature *variation* around the modified annual and daily average temperatures along this section of the river (Braun 2015a). Appropriate *changes* in water temperature consequently do occur to trigger spawning. No further information has emerged on the possible role of the photoperiod in triggering spawning (Hoffnagle et al. 1999; Robinson et al. 1998).

Updates to Chapter 5 – Controlling Factors

CHANNEL AND OFF-CHANNEL ENGINEERING

No change.

FLSU MONITORING AND CONSERVATION PROGRAMS

This is a new controlling factor for the FLSU conceptual ecological model, added to ensure that the CEM better captures the key drivers of habitat manipulation; the new habitat element, “Genetic Diversity”; and the updated habitat element, “Monitoring, Capture, Handling” (formerly “Scientific Study”). The definition for this new controlling factor is as follows:

The controlling factor, “FLSU Monitoring and Conservation Programs,” addresses the activities of Reclamation, the USFWS, and the States and Tribes in monitoring FLSU and managing its habitat in the LCR below Lake Mead. Those actions for which the LCR MSCP has lead responsibility are guided specifically by the LCR MSCP Habitat Conservation Plan, approved in 2004 (LCR MSCP 2004). The LCR MSCP annually publishes a combined final implementation report, fiscal year work plan and budget, and accomplishment report for the previous fiscal year (e.g., LCR MSCP 2018) that describes, in detail, the activities of the program.

LCR MSCP efforts concerning FLSU along the LCR have focused on monitoring, including the introduction of PIT-tagged FLSU for telemetric tracking in Reach 3 between Davis Dam and Lake Havasu (see chapter 4, “Monitoring, Capture, Handling”) and on habitat protection (LCR MSCP 2018). Beginning in 2018, the monitoring of FLSU in the LCR is no longer separately budgeted under the LCR MSCP annual work plan (LCR MSCP 2018). However, monitoring of FLSU regularly occurs as a consequence of LCR MSCP monitoring of RASU and BONY, and this practice will continue (LCR MSCP 2018). Similarly, the LCR MSCP monitors water chemistry parameters and body loads of selenium in phytoplankton, macroinvertebrates, and non-native fishes (see chapter 4, “Water Chemistry”). The LCR MSCP also monitors avian feeding on RASU and BONY along the LCR, including in Laughlin Lagoon. These monitoring activities provide crucial information on habitat conditions that affect not only RASU and BONY but also FLSU. Finally, habitat management for RASU (and, in the future, potentially BONY as well) along the LCR main stem and connected backwaters necessarily benefit FLSU as well.

NON-FLSU FISHERIES

This controlling factor replaces the original controlling factor, "Fishing Activity and Fisheries Management," with a slightly updated definition as follows:

This factor addresses State management of fisheries along the LCR, other than for FLSU, including management of sport fishes and other fish species covered under the LCR MSCP Habitat Conservation Plan (LCR MSCP 2004). The States bordering the LCR recognize and oversee the sport fisheries for introduced fishes along the river, its reservoirs and connected backwaters, and its tributaries. The fishes recognized by these States as sport fishes include intentionally introduced and/or stocked species and accidental introductions. The States and recreational fishers have also introduced bait and forage species to support the sport fisheries. These bait and forage species may be caught as sport fishes and may also be considered (by the States) to be nuisance species. Arizona lists the official sport fishes for the State and State records for any caught along the LCR (https://fishaz.azgfd.com/).

Management of sport fisheries includes regulating fishing activities and introducing and/or stocking sport species as well as bait and forage species for the sport fisheries. These management activities and the legacies of past such activities may affect the LCR ecosystem in several ways, including introducing infectious agents, shaping public perceptions of the relative value of sport fisheries versus native species recovery programs, shaping the spectrum of species that prey on or compete with FLSU, and altering physical habitat. The potential for conflicts between sport fishery management and the conservation of native fishes along the Colorado River in fact is a longstanding concern (Clarkson et al. 2005; Holden 1991; Marsh and Pacey 2005; Minckley 1991; Minckley et al. 2003; Mueller and Marsh 2002; NRC 1991; Rolston, III 1991). Table 3 updates the list of non-native sport species—and species introduced as bait or forage species for the sport fisheries—introduced into and known to still occur in the LCR ecosystem. Table 3 also indicates whether each species is known to prey on or compete with FLSU or could be proposed as predators or competitors based on their feeding ecology. Infectious (including parasitic) organisms that are known to infect FLSU and likely introduced with non-native sport fishes include anchor worms and ich (see chapter 4, "Infectious Agents").

The States of the LCR and Federal agencies overseeing the LCR also manage the populations of several native species other than FLSU. Three of these are covered under the Habitat Conservation Plan (LCR MSCP 2004)—BONY, humpback chub, and RASU—and one, roundtail chub, 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 the dominant native aquatic predator of FLSU.

Recreational fishers also could have effects on FLSU. However, as noted in chapter 4 of the original FLSU conceptual ecological model (Braun 2015a), anglers do not specifically target FLSU. On the other hand, anglers also are known to transplant desired sport or forage/bait fishes to waterbodies where they appear to be absent. Mueller and Wydoski (2004) hypothesize that this was the source of isolated instances of FLSU observed along the LCR prior to 1976.

MOTORBOAT ACTIVITY

No change.

NUISANCE SPECIES INTRODUCTION AND MANAGEMENT

No change.

TRIBUTARY INFLOWS

No change.

WASTEWATER AND OTHER CONTAMINANT INFLOWS

No change.

WATER STORAGE-DELIVERY SYSTEM DESIGN AND OPERATIONS

This controlling factor replaces the original controlling factor, “Water Storage/Delivery System Design and Operations,” to standardize naming conventions across all LCR MSCP conceptual ecological models.

Updates to Chapter 6 – Conceptual Ecological Model by Life Stage

The following sections identify all changes made to the FLSU conceptual ecological model workbook other than changes that involve only updates to names. These latter changes are listed separately in table 5 (see "Summary of Standardization of Terms," this chapter). The items in each subsection below are arranged alphabetically. The abbreviations, CF for controlling factor, HE for habitat element, CAP for critical activity or process, and LSO for life-stage outcome are provided to identify component types where needed. Each item also identifies the life stage(s) to which the item applies.

NEW LINKS WITH CONTROLLING FACTORS AS CAUSAL AGENTS

- FLSU Monitoring and Conservation Programs (CF) effects on Channel and Off-Channel Engineering (CF): The LCR MSCP and its partners can and sometimes do modify channel and off-channel physical habitat in the interests of meeting LCR MSCP goals or conducting experiments (e.g., pond fertilization). However, the LCR MSCP presently has no plans for such management in support of FLSU conservation (LCR MSCP 2018). Link intensity has the potential to be high but presently is low, given the absence of plans for such efforts, and spatial and temporal scales presently are low. Opportunities for such manipulation are spatially and temporally predictable, but intensity can vary unpredictably. The processes involved are well understood. *Applies to all life stages.*

- FLSU Monitoring and Conservation Programs (CF) effects on Aquatic Macrophytes (HE): Aquatic macrophyte management potentially could affect the distribution and density of such vegetation along shorelines and in connected backwaters along the Colorado River between Davis Dam and Lake Havasu. However, the LCR MSCP presently has no plans for such management (LCR MSCP 2018). Link intensity has the potential to be high, but presently is low, given the absence of plans for such efforts, and spatial and temporal scales presently are low. Opportunities for such manipulation are spatially and temporally predictable, but intensity can vary unpredictably. The processes involved are well understood. *Applies to all life stages.*

- FLSU Monitoring and Conservation Programs (CF) effects on Genetic Diversity (HE): Annual introductions of FLSU from Lake Mead (after rearing to subadult or adult size: see chapter 3, "Genetic Diversity") potentially have affected and could continue to affect genetic diversity among FLSU between Davis Dam and Lake Havasu. The annual introductions of PIT-tagged FLSU supported telemetric studies of FLSU habitat use and movement. However, the most recent LCR MSCP work plan (LCR MSCP 2018) does not include plans for continued monitoring of FLSU below Davis Dam, and it lists the telemetric studies as completed. This proposed causal link nevertheless has had some positive but unmeasured intensity in the past, and these effects will persist for some unknown time and presumably affect all FLSU habitat between Davis Dam and Lake Havasu. Predictability is high but understanding is low concerning the consequences of the introductions for FLSU genetic diversity along this section of the river. *Applies to all life stages*.

- FLSU Monitoring and Conservation Program (CF) effects on Infectious Agents (HE): The stocking of FLSU into Reach 3 from hatcheries (where the FLSU were reared after capture in Lake Mead) provides a potential mechanism for the spread of infectious agents into the LCR depending on hatchery conditions. However, hatcheries do their best to prevent the spread of such agents and especially to ensure that released cohorts to not carry these agents with them. Hatcheries maintain a complex suite of protocols for controlling the spread of infectious agents within and beyond their facilities and monitor cohorts regularly to ensure that cohorts do not carry agents with them upon release. Link intensity and temporal scales are hypothesized to be low given the control that hatcheries exert over infectious agents, but spatial scale is hypothesized to be medium since any introduction into the LCR could spread at least between Davis Dam and Lake Havasu. However, hatcheries do their best to prevent the spread of such agents, and especially to ensure that released cohorts to not carry these agents with them, resulting in high predictability, and hatchery methods for controlling infectious agents and their effectiveness are well known. *Applies to all life stages*.

- FLSU Monitoring and Conservation Program (CF) effects on Monitoring, Capture, Handling (HE): The LCR MSCP has lead responsibility for all monitoring of FLSU between Davis Dam and Lake Havasu, and has carried out several years of such monitoring under various components of its annual work plans (LCR MSCP 2018). However, the most recent LCR MSCP work plan (LCR MSCP 2018) includes no plans for continued monitoring of FLSU below Davis Dam, and it lists all previous monitoring tasks as completed as of 2018. Monitoring of FLSU will continue only as a consequence of ongoing monitoring of RASU and BONY. Link intensity, spatial extent, and temporal extent therefore are low and predictability and understanding high. *Applies to all life stages.*

NEW LINKS WITH HABITAT ELEMENTS AS CAUSAL AGENTS

- Birds and Mammals (HE) effects on Predation (CAP) for FLSU eggs and protolarvae: The original FLSU conceptual ecological model did not include this link, as there was no evidence pertaining to bird or mammal predation on this life stage. However, the expanding knowledge of at least avian predation on later life stages suggests that at least some wading birds should be fully capable of feeding on FLSU protolarvae. The text and ratings for this new link (for eggs and protolarvae) follow those in the equivalent links for the later life stages but with qualification that this relationship is hypothesized for eggs and protolarvae but not documented. *Applies only to Eggs and Protolarvae, for which this is a new link.*

- Genetic Diversity (HE) effects on Chemical Stress (CAP): This link identifies one possible way in which genetic diversity could affect FLSU in the LCR between Davis Dam and Lake Havasu by shaping their ability to respond to potentially chemically stressful conditions such as exposure to anthropogenic contaminants. The genetic diversity of a population affects its resilience in the face of variation in water chemistry—the greater the genetic diversity, the greater the likelihood that portions of the population will be able to tolerate or adapt to changes in water chemistry and also pass this ability on to the next generation. The hypothesized link is proposed to be negative (no thresholds known) and unidirectional, with unknown intensity and high spatial and temporal scales. The link magnitude reason notes that, theoretically, this relationship could be important, but the literature does not indicate whether or how it may matter for FLSU. The spatial and temporal scale ratings are potentials. Link predictability and understanding are both low. *Applies to all life stages*

- Genetic Diversity (HE) effects on Disease (CAP): This link identifies one possible way in which genetic diversity could affect FLSU in the LCR between Davis Dam and Lake Havasu by shaping their ability to respond to new or established disease agents. The genetic diversity of a population affects its resilience in the face of pathogens—the greater the genetic diversity, the greater the likelihood that portions of the population will have resistance to or be able to recover successfully from novel pathogens and also pass this ability on to later generations. The hypothesized link is proposed to be negative (no thresholds known) and unidirectional, with the link character reasoning noting that the fact that genetic diversity can affect susceptibility to disease is well established but the ways in which this occurs are complex. The link is proposed to have unknown intensity and high spatial and temporal scales, with the link magnitude reason stating that, theoretically, this relationship is important, but the literature does not indicate whether or how it may matter for FLSU health and survivorship. The spatial and temporal scale ratings are potentials. Link predictability is low: Theoretically, this relationship is important, but the literature does not indicate whether or how it may matter for FLSU health and survivorship. More importantly for predictability, the incidence of disease among FLSU in the LCR probably depends on many factors, of which genetic diversity is but one. Link understanding similarly is low: Theoretically, this relationship is important, but the literature does not indicate whether or how it may matter for FLSU health and survivorship. *Applies to all life stages.*

- Genetic Diversity (HE) effects on Swimming (CAP): This link identifies one possible way in which genetic diversity could affect FLSU in the LCR between Davis Dam and Lake Havasu by shaping their swimming morphology and/or performance characteristics. The genetic diversity of a fish population affects the range of potential variation in swimming morphology and/or performance characteristics in the population – the greater the genetic diversity, the greater these range of variation that can be passed on to later generations. The hypothesized link is proposed to have unknown character, but is assumed to be unidirectional, with unknown intensity, spatial scale, and temporal scale. The link magnitude reason states that, theoretically, this relationship could be important, but the possible effects of genetic diversity on FLSU swimming morphology and abilities are unknown. Link predictability consequently is unknown and link understanding low. *Applies to all life stages* ***except*** *Eggs and Early Larvae.*

- Genetic Diversity (HE) effects on Thermal Stress (CAP): This link identifies one possible way in which genetic diversity could affect FLSU in the LCR between Davis Dam and Lake Havasu by shaping their ability to respond to potentially thermally stressful conditions or the ways in which physical characteristics such as embryo maturation rates, swimming stamina, or swimming strength may vary with water temperature. The genetic diversity of a population affects its resilience in the face of temperature variation—the greater the genetic diversity, the greater the likelihood that portions of the population will be able to tolerate or even benefit from altered water temperatures. The hypothesized link is proposed to be negative (with no known threshold) and unidirectional. Link intensity is unknown with high spatial and temporal scales. The link magnitude reason states that, theoretically, this relationship could be important, but the literature does not indicate whether and how it actually matters for FLSU. The spatial and temporal scale ratings are potentials. Link predictability consequently is unknown and link understanding is necessarily rated as low. *Applies to all life stages.*

- Turbidity (HE) effects on Birds and Mammals (HE): This link refers to the possible effects of turbidity on where birds and mammals position themselves within the LCR ecosystem. Piscivorous birds and mammals presumably concentrate their attention on less-turbid locations, where they are more able to see potential prey in the water. Beavers and muskrats also may prefer waters with lower turbidity, in their cases for navigating or simply because the vegetation they prefer occurs more plentifully in settings with lower turbidity. However, these relationships have not been studied along the LCR. The hypothesized link is proposed to be negative (with no known threshold) and unidirectional. Link intensity is unknown. Link spatial scale is proposed to be low but temporal scale high. The link magnitude reason states that, while this relationship could have significant impact, these relationships have not been studied along the LCR. Further, most locations in the LCR ecosystem have low turbidity due to river regulation, and beavers and muskrats may also have limited distributions, limiting the spatial scale of any possible relationships. On the other hand, if active, these relationships should apply at all times of the year, through all years. Link predictability consequently is unknown and link understanding is necessarily rated as low. *Applies to all life stages.*

- Water Flow, Turbulence (HE) effects on Spawning Adult Fertility (LSO): This link refers to the possible effects of flow on fertility. The factors affecting fertility among FLSU may be similar (by analogy) to that among BONY, for which Osborne and Turner (2017) note that "patterns of water flow can also affect reproductive success because flow can transport, mix and dilute gametes. For this reason, it is possible that the high degree of reproductive success [for BONY in 2014–17] may be higher in the backwaters than in lotic systems." The hypothesized link is proposed to be negative (with no known threshold) and unidirectional. Link intensity is unknown, but both link spatial scale and temporal scale are rated high. Theoretically, this relationship could be important, but at present, it has been hypothesized but not formally assessed by experiments, so the intensity of effect is unknown. The spatial scale would apply to all sites where FLSU attempt to spawn and to all times when spawning occurs. Link predictability consequently is unknown and link understanding is necessarily rated as low. *Applies only to Spawning Adults*.

UPDATED LINKS WITH HABITAT ELEMENTS AS CAUSAL AGENTS

- Aquatic Macrophyte (HE) effects on Resting/Hiding (CAP). *Link understanding rating updated to medium* given the increasing evidence that FLSU seek the cover of aquatic macrophytes, particularly bulrush and particularly during daylight hours. Limited spatial availability of such cover remains the main constraint on overall magnitude of effect, as indicated in the original FLSU conceptual ecological model. *Applies to all life stages* ***except*** *Eggs and Protolarvae, for which this relationship is not relevant.*

- Birds and Mammals (HE) effects on Predation (CAP): *Link intensity updated to High* based on new evidence of how severe this link can be, in absence of protective turbidity or vegetative cover. *Link understanding rating updated to medium* based on accumulating evidence. *Applies to all life stages* ***except*** *Eggs and Protolarvae, for which this is a* ***new*** *link.*

- Monitoring, Capture, Handling (HE) effect on Mechanical Stress (CAP): *Link reason text updated* with information from updated habitat element definition (see chapter 4). Link ratings remain unchanged. *Applies to all life stages.*

- Turbidity (HE) effects on Aquatic Macrophytes (HE): *Link character direction updated to bi-directional. Link reason and link character reason are updated with the following:* Reciprocally, aquatic macrophytes dampen wave action, flow velocities, and turbulence, allowing suspended matter to settle out, reducing turbidity in those settings. *Applies to all life stages.*

- Turbidity (HE) effects on Predation (CAP): *Link intensity updated to high*, and *link predictability updated to medium*, based on evidence that avian predators and most aquatic predators of the LCR cannot hunt effectively in turbid water: Turbidity has well-known inhibiting effects on avian piscivory in freshwater ecosystems in general (Cezilly 1992) and on predation by sight-hunting fishes (Vaage et al. 2015; Ward et al. 2016). However, smallmouth bass readily tolerate moderate turbidity (Bestgen et al. 2011). As noted above, depredation by flathead catfish appears to be relatively unaffected by turbidity (e.g., Vaage et al. 2015), and flatheads may actually prefer habitats with higher turbidity and/or similar cover (Humphrey et al. 2016). The limited spatial and temporal availability of sufficient turbidity in habitat zones of interest to FLSU remains the main constraint on overall magnitude of effect. *Link reason updated accordingly*. *Link understanding rating remains low*. *Applies to all life stages*. The link magnitude reason statement is also updated as stated earlier in this paragraph, with a similar modification to the link predictability reason.

- Turbidity (HE) effects on Resting/Hiding (CAP): *Link intensity updated to high* based on increasing evidence that FLSU actively seek or remain in turbid water when apparently trying to hide from threats and will preferentially move into turbid waters during daylight hours even when aquatic macrophyte cover is also immediately available. The limited spatial and temporal availability of sufficient turbidity in habitat zones of interest to FLSU remains the main constraint on the overall magnitude of effect. *Link reason and link magnitude reasoning updated accordingly*. *Link understanding rating updated to medium*. *Applies to all life stages **except** (1) Eggs and Protolarvae and (2) Spawning Adults, for which Resting/Hiding is not a valid critical biological activity or process.* The link magnitude reason is also updated to note that FLSU evolved in a natural system with frequent, widespread, persistent turbidity, and therefore, their repertoire of behaviors for finding suitable resting/hiding locations must include behaviors that take turbidity into account. Ample evidence documents FLSU use of turbid waters as cover for resting/hiding habitat. However, episodes of high turbidity in today's regulated river and isolated ponds are localized and mostly brief and therefore probably do not test the limits of FLSU behaviors in response to turbidity. In settings where extended pulses of turbidity still occur, the intensity of this relationship would likely be greater.

- Water Depth (HE) effects on Aquatic Macrophytes (HE): *Link character direction updated to bi-directional* since aquatic macrophytes trap suspended sediment, which results in the accumulation of sediment as a corollary of the reduction in turbidity. *Link reason and link magnitude reason updated accordingly*. All other fields remain unchanged. *Applies to all life stages.*

- Water Flow, Turbulence (HE) effects on Aquatic Macrophytes (HE): *Link character direction updated to bi-directional* since aquatic macrophytes dampen wave action, flow velocities, and turbulence in those settings. *Link reason and link magnitude reasoning updated accordingly*. *Link intensity updated to high*. All other fields remain unchanged. *Applies to all life stages.*

NEW LINKS WITH CRITICAL ACTIVITIES/PROCESSES AS CAUSAL AGENTS

- Chemical Stress (CAP) effects on new "… Growth" life-stage outcome for Eggs and Protolarvae, Fry and Early Juveniles, Older Juveniles and Subadults, and Adults: These links recognize that chronic chemical stress can impair FLSU body condition and inhibit FLSU growth. Chronic chemical stress is a commonly recognized cause of impaired body condition in fishes. The hypothesized link is proposed to be negative (with no known threshold) and bi-directional because chronic stress can reduce growth, and impaired condition can increase susceptibility to stress. Link intensity is proposed to be high but with low spatial and temporal scales because, while chronic chemical stress is a commonly recognized cause of impaired body condition and growth in fishes, FLSU in the LCR ecosystem face few or no situations in which they experience chronic chemical stress. Correspondingly, link predictability and understanding are rated as high. *Applies to all life stages **except** Spawning Adults.*

- Disease (CAP) effects on new "… Growth" life-stage outcome for Eggs and Protolarvae, Fry and Early Juveniles, Older Juveniles and Subadults, and Adults: These links recognize that chronic illness can impair FLSU body condition and inhibit FLSU growth. Chronic illness is a commonly recognized cause of impaired body condition in fishes. The hypothesized link is proposed to be negative (with no known threshold) and bi-directional because chronic stress can reduce growth and impaired condition can increase susceptibility to stress. Link intensity, spatial scale, and temporal scale are all proposed to be low: Chronic illness is a commonly recognized cause of impaired body condition and growth in fishes, and FLSU are susceptible to several known pathogens in the LCR ecosystem. However, several studies have been observed that, while showing signs of infection, FLSU did not appear to be debilitated by their disease loads (Joseph et al. 1977; Flagg 1982). Correspondingly, link predictability and understanding are rated as high. *Applies to all life stages **except** Spawning Adults.*

- Foraging (CAP) effects on new "… Growth" life-stage outcome for Fry and Early Juveniles, Older Juveniles and Subadults, and Adults: These links recognize that foraging success affects FLSU body condition and growth. Foraging success is a commonly recognized cause of healthy body condition in fishes. *Applies to all life stages **except** Spawning Adults and has very limited, low-intensity relevance for Eggs and Protolarvae.* The hypothesized link for FLSU fry and early juveniles, older juveniles and subadults, and adults, for which body condition presumably varies with foraging success (Froese 2006; Hayes et al. 2017; Nash et al. 2006). The link for these life stages is hypothesized to be positive (with no known threshold) and bi-directional because foraging success in these life stages promotes growth and healthy body condition, and impaired body condition can reduce foraging success. Link intensity, spatial scale, and temporal scale for these life stages are all rated as high: Foraging success is a commonly recognized cause of healthy body condition in fishes. Correspondingly, link predictability and understanding are rated as high. The link reason for FLSU eggs and protolarvae alternatively notes that FLSU protolarvae still retain some yolk and forage very little, with ratings accordingly.

- Hybridization (CAP) affects Genetic Diversity (HE) for all five life stages: These links recognize that FLSU hybridization with RASU could affect FLSU (and RASU) genetic diversity between Davis Dam and Lake Havasu, as is the case in Lake Mead and the Grand Canyon. The hypothesized link is proposed to be complex and unidirectional, with low intensity, spatial scale, and temporal scale, with the link magnitude reason referring readers to the discussion in chapter 3, (see "Hybridization"). Link predictability is unknown because the circumstances in which FLSU-RASU hybridization might predictably affect genetic diversity in the wild are not well understood, although it is known that FLSU and RASU apparently spawn in the same kinds of locations at overlapping times. Link understanding correspondingly is low. *Applies to all life stages.*

- Hybridization (CAP) affects Competition (CAP) for all five life stages: FLSU hybrids with other catostomids potentially may compete with non-hybrid FLSU for food or physical habitat. For example, Anderson and Stewart (2007) found that, unlike native catostomids, the non-native white sucker and its hybrids can persist in western Colorado regardless of alterations to the flow regime, giving them an advantage over the native suckers. Studies of the possible demographic and ecological consequences of hybridization between FLSU and RASU are ongoing (Wolters et al. 2016, 2017). The hypothesized link is proposed to be positive (with no known threshold) and unidirectional – the higher the frequency of hybrids along a given section of the river, the greater the competition that pure FLSU will experience from hybrids. Link intensity is unknown, but spatial and temporal scales ratings are proposed to be low. Hybridization of FLSU with other catostomids occurs in the UCRB, where all three of the other species occur, with which FLSU can hybridize: the native RASU and bluehead sucker, and the non-native white sucker. However, among these species, only RASU occur in the LCR reach occupied by FLSU, where low RASU numbers limit opportunities for crosses. Link predictability is low because of the low numbers of RASU in the single LCR reach occupied by FLSU and the lack of knowledge of whether or how hybrids may compete with FLSU. Link understanding correspondingly also is low. *Applies to all life stages.*

- Mechanical Stress (CAP) effects on new "… Growth" life-stage outcome for Eggs and Protolarvae, Fry and Early Juveniles, Older Juveniles and Subadults, and Adults: These links recognize that chronic mechanical stress can inhibit FLSU growth. Chronic mechanical stress, including excessive energy expenditure in physically difficult environments, is a commonly recognized cause of impaired body condition in fishes. The hypothesized link is proposed to be negative (with no known threshold) and bi-directional: Chronic mechanical stress can reduce growth, and impaired condition can increase susceptibility to stress. Link intensity is hypothesized to be high but with low spatial and temporal scales: Chronic mechanical stress is a commonly recognized cause of impaired body condition and growth in fishes. However, FLSU in the LCR ecosystem face few or no situations in which they experience chronic mechanical stress. Correspondingly, both link predictability and understanding are high. *Applies to all life stages* ***except*** *Spawning Adults.*

- Resting/Hiding (CAP) effects on Monitoring, Capture, Handling (HE) in all motile life stages: FLSU resting/hiding behavior in all motile life stages potentially could affect the likelihood of their detection and/or capture during monitoring. This relationship potentially exists because the detection rates of different tracking methods (e.g., PIT tag monitoring) may differ when fish are at lesser versus greater depth, out in open water versus hiding in cover habitat, or moving in or out of turbid waters (see chapter 4, "Turbidity"). The likelihood of capture by different methods (e.g., by electrofishing or various net-based methods) may vary for similar reasons. These relationships are suggested based on evidence from studies of the humpback chub (Yackulic et al. 2018). Conversely, efforts to capture fishes may cause them to flee, resulting in a bi-directional relationship. For example (see chapter 4, "Monitoring, Capture, Handling"), telemetric monitoring of PIT-tagged FLSU released below Davis Dam found that detection of FLSU with antenna arrays was noticeably more difficult when the FLSU moved into the cover of bulrush stands during the daylight hours (LCR MSCP 2018). The hypothesized link is proposed to be complex because of the range of behaviors and effects potentially involved, and bi-directional because of the feedback relationship. Link intensity and predictability are unknown, and link understanding is low, because the relationship has not been systematically studied for FLSU. However, link spatial and temporal scales are hypothesized to be high because the relationship should apply wherever and whenever FLSU monitoring takes place. *Applies to all life stages* ***except*** *Eggs and Protolarvae.*

- Swimming (CAP) effects on Monitoring, Capture, Handling (HE) in all motile life stages: FLSU swimming behavior in all motile life stages potentially could affect the likelihood of their detection and/or capture during monitoring. This relationship potentially exists because the detection rates of different tracking methods (e.g., PIT tag monitoring) may differ when fish are at lesser versus greater depth, out in open water versus hiding in cover habitat, or moving in or out of turbid waters (see chapter 4, "Turbidity"). The likelihood of capture by different methods (e.g., by electrofishing or various net-based methods) may vary for similar reasons. These relationships are suggested based on evidence from studies of the humpback chub (Yackulic et al. 2018). Conversely, efforts to capture fishes may cause them to flee, resulting in a bi-directional relationship. For example (see chapter 4, "Monitoring, Capture, Handling"), telemetric monitoring of PIT-tagged FLSU released below

Davis Dam found that detection of the FLSU with antenna arrays was noticeably more difficult when the FLSU moved into the cover of bulrush stands during the daylight hours (LCR MSCP 2018). The hypothesized link is proposed to be complex because of the range of behaviors and effects potentially involved, and bi-directional because of the feedback relationship. Link intensity and predictability are unknown, and link understanding is low, because the relationship has not been systematically studied for FLSU. However, link spatial and temporal scales are hypothesized to be high because the relationship should apply wherever and whenever FLSU monitoring takes place. *Applies to all life stages* ***except*** *Eggs and Protolarvae*.

- Thermal Stress (CAP) effects on new "… Growth" life-stage outcome for Eggs and Protolarvae, Fry and Early Juveniles, Older Juveniles and Subadults, and Adults: These links recognize that chronic thermal stress can inhibit FLSU growth. Chronic thermal stress, including excessive energy expenditure in thermally difficult environments, is a commonly recognized cause of impaired body condition in fishes. The hypothesized link is proposed to be negative (with no known threshold) and bi-directional: Chronic thermal stress can reduce growth, and impaired condition can increase susceptibility to stress. Link intensity is hypothesized to be high but with low spatial and temporal scales: Chronic thermal stress is a commonly recognized cause of impaired body condition and growth in fishes. However, FLSU in the LCR ecosystem face few or no situations in which they experience chronic thermal stress, although the range of variation (minima, maxima, average) in water temperatures below Davis Dam does not resemble the natural temperature regime. Correspondingly, both link predictability and understanding are high. *Applies to all life stages* ***except*** *Spawning Adults*.

DELETED LINKS WITH CRITICAL ACTIVITIES/PROCESSES AS CAUSAL AGENTS

- Effects of Chemical Stress, Disease, Foraging, Mechanical Stress, and Thermal Stress [(CAP); n = 5 links] on Adult Reproductive Participation (LSO): These links are replaced with links from these causal agents to Adult Growth, as described above, and an added link from Adult Growth to Adult Reproductive Participation, as described below. *Applies only to Adults.*

- Effects of Predation (CAP) on Adult Reproductive Participation (LSO): This link is no longer needed because Predation affects Adult Survival, and the update adds a link from Adult Survival to Adult Reproductive Participation, as described below. *Applies only to Adults.*

- Effects of Predation (CAP) on Spawning Adult Fertility (LSO): This link is no longer needed because Predation affects Spawning Adult Survival, and the update adds a link from Spawning Adult Survival to Spawning Adult Fertility, as described below. The CEM also retains links from Chemical Stress, Disease, Foraging, Mechanical Stress, and Thermal Stress to Spawning Adult Fertility because this is a direct effect of stress, not mediated by growth or condition. *Applies only to Spawning Adults.*

UPDATED LINKS WITH CRITICAL ACTIVITIES/PROCESSES AS CAUSAL AGENTS

- Alongside the above new bi-directional linkages from "…growth" to Chemical Stress, Disease, Foraging, Mechanical Stress, Thermal Stress, the CEM retains the original causal linkages from these five critical activities or processes to the "…Survival" outcomes for *all five life stages except Spawning Adults. However, the effects of Foraging on Egg and Protolarval Survival are minimal because FLSU protolarvae forage very little*. The model retains these direct causal linkages because unsuccessful foraging and these four forms of stress can **either** (1) impede growth or reduce reproductive participation via chronic stress, as recognized in the five new links listed above, **or** (2) cause mortality (acute stress). The link reasons for the causal relationships from the five critical activities or processes to the respective "…Survival" outcomes are updated to include this latter statement, contrasting chronic with acute stress, so that these original links are identified as focusing on acute stress only.

NEW LINKS WITH LIFE-STAGE OUTCOMES AS CAUSAL AGENTS

- "… Growth" life-stage outcome effects on Predation (CAP): Links are added *from Fry and Early Juvenile Growth, Older Juvenile and Subadult Growth, and Adult Growth (new LSOs*) for all three life stages. The idea here is that FLSU vulnerability to predation may depend, in part, on body size, as discussed in the original FLSU conceptual ecological model. Size depends on growth: Adults that grow more slowly spend more time as smaller adults, potentially increasing their exposure to predation. Further, as a result of their relative physical weakness, individual fry, juveniles, subadults, and adults that do not experience growth sufficient to maintain or quickly return to good body condition following some disturbance may be more vulnerable to predation or less able to avoid or escape extreme flow disturbances. A study of trophic relationships among Colorado pikeminnow and its prey in the San Juan River (Franssen et al. 2006) noted FLSU larvae grow larger faster than do the larvae of either RASU or BONY (LCR MSCP 2008; McAda and Wydoski 1985; Robinson and Childs 2001; Snyder and Muth 2004; Sweet et al. 2009; Walters et al. 2006, 2012). This faster growth rate conceivably helps FLSU larvae and fry "run the gauntlet" of spring predators better than do RASU or BONY. The hypothesized relationship is proposed to be negative (with no known threshold) and unidirectional. The intensity of the relationship is not presently known and is not presently a subject of study by the LCR MSCP (LCR MSCP 2018). However, Riedel et al. (2007) found that avian predators at the Salton Sea tended to avoid eating larger fishes, but also preferred slender-bodied fishes over deep-bodied ones, and FLSU has a slender body form. Unlike some other native fishes of the Colorado River Basin, FLSU lack morphological features that would have discouraged pikeminnow predation (Franssen et al. 2007; Portz and Tyus 2004). The available information therefore suggests a rating of high for both spatial and temporal scales, with unknown predictability and low understanding. *Applies only to Fry and Early Juveniles, Older Juveniles and Subadults, and Adults*.

- "… Growth" life-stage outcome effects on Swimming (CAP): Links are added *from Fry and Early Juvenile Growth, Older Juvenile and Subadult Growth, and Adult Growth (new LSOs*). The idea here is that growth and good body condition result in a greater ability to flee or avoid potentially harmful conditions, as indicated in studies of swimming performance that show greater strength with greater body size. The evidence from studies of FLSU swimming performance, together with the basic concepts underlying the use of Condition Factor (Froese 2006; Nash et al. 2006), suggest that FLSU swimming performance likely varies with body condition. The hypothesized link therefore is proposed to be positive (with no known threshold) and unidirectional, with high intensity, spatial scale, and temporal scale, simply because FLSU swimming performance likely varies with body condition in all of these life stages. Correspondingly, both link predictability and understanding are rated high. *Applies only to Fry and Early Juveniles, Older Juveniles and Subadults, and Adults*.

- "… Growth" life-stage outcome effects on "… Survival" outcomes: Links added from *Egg and Protolarval Growth, Fry and Early Juvenile Growth, Older Juvenile and Subadult Growth, and Adult Growth (new LSOs)* ***to*** *Egg and Protolarval Survival, Fry and Early Juvenile Survival, Older*

Juvenile and Subadult Survival, and Adult Survival, respectively. For the eggs and protolarvae, the idea here is that the longer the duration of the life stage (due to slower growth), the longer the eggs and protolarvae are vulnerable to lethal harm from various sources. For the three later life stages (excluding spawning adults), the idea here is that greater size conveys lower vulnerability to predation as well as greater ability to avoid or escape from other threats/stresses. Especially for adults, growth above a size threshold could reduce vulnerability to most aquatic predators. The hypothesized link therefore is proposed to be positive (with no known threshold) and bi-directional: Longer survival reciprocally permits greater growth. Link intensity, spatial scale, and temporal scale are all rated as high: The relationship is expected to be strong, based on core biological principles, and FLSU appear not only to be maintaining their abundance between Davis Dam and Lake Havasu but to be maintaining or increasing their abundance in Lake Mead and the Grand Canyon. Correspondingly, both link predictability and understanding are rated high. *Applies to all life stages except Spawning Adults*.

- Adult Growth (new LSO) effect on Adult Reproductive Participation (LSO): *A link is added between these two life-stage outcomes, with Adult Growth as the causal agent*. The idea here is that growth is a covariate of the acquisition of the energy stores needed to support participation. The CEM assumes that adults with poorer condition are less likely to experience gonadal maturation and/or less likely to respond to spawning cues and/or be less likely to compete successfully during mating. The hypothesized relationship is proposed to be positive (with no known threshold) and unidirectional. Link intensity, spatial scale, and temporal scale are all rated as high: The relationship is expected to be strong, based on core biological principles, and should be active in every setting where FLSU occur in or are linked to the LCR, including between Davis Dam and Lake Havasu and in Lake Mead and the Grand Canyon. Correspondingly, both link predictability and understanding are rated high. *Applies only to Adults*.

- Adult Survival (LSO) effect on Adult Reproductive Participation (LSO): *A link is added between these two life-stage outcomes, with Adult Survival as the causal agent*. The idea here is that only adults that survive can participate in reproduction. The hypothesized relationship is proposed to be positive (with no known threshold) and unidirectional. Link intensity, spatial scale, and temporal scale are all rated as high based on basic biological principles. Correspondingly, both link predictability and understanding are rated high. *Applies only to Adults*.

- Spawning Adult Survival (LSO) effect on Spawning Adult Fertility (LSO): *A link is added between these two life-stage outcomes, with Spawning Adult Survival as the causal agent*. The idea here is that only adults that survive contribute to overall fertility of spawning adults. The hypothesized relationship is proposed to be positive (with no known threshold) and unidirectional. Link intensity, spatial scale, and temporal scale are all rated as high based on basic biological principles. Correspondingly, both link predictability and understanding are rated high. *Applies only to Spawning Adults*.

SUMMARY OF STANDARDIZATION OF TERMS

(Items highlighted in blue were added or revised for 2018).

Table 5.—(New table for this update): Updated FLSU conceptual ecological model component names

FLSU conceptual ecological model updated terms, 2018	FLSU conceptual ecological model original terms, 2015
Life stages	
Eggs and Protolarvae	Eggs and Protolarvae
Fry and Early Juveniles	Fry and Early Juveniles
Older Juveniles and Subadults	Older Juveniles and Subadults
Adults	Adults
Spawning Adults	Spawning Adults
Life-stage outcomes	
Egg and Protolarval Survival	Egg and Protolarval Survival Rate
Egg and Protolarval Growth	(new)
Fry and Early Juvenile Survival	Fry and Early Juvenile Survival Rate
Fry and Early Juvenile Growth	(new)
Older Juvenile and Subadult Survival	Older Juvenile and Subadult Survival Rate
Older Juvenile and Subadult Growth	(new)
Adult Survival	Adult Survival Rate
Adult Growth	(new)
Adult Reproductive Participation	Adult Reproductive Participation Rate
Spawning Adult Survival	Spawning Adult Survival Rate
Spawning Adult Fertility	Spawning Adult Fertility Rate
Critical biological activities and processes	
Chemical Stress	Chemical Stress
Competition	Competition
Disease	Disease
Drifting	Drifting
Egg Settling and Adhesion	Egg Settling and Adhesion
Foraging	Foraging
Hybridization	Hybridization
Mechanical Stress	Mechanical Stress
Predation	Predation
Resting/Hiding	Resting
Swimming	Swimming
Thermal Stress	Thermal Stress
Habitat elements	
Aquatic Macrophytes	Aquatic Macrophytes
Aquatic Vertebrates	Aquatic Vertebrates
Birds and Mammals	Birds and Mammals
Fishing Encounters	Fishing Encounters
Genetic Diversity	(new)
Infectious Agents	Infectious Agents
Invertebrates and POM	Invertebrates and POM
Macrohabitat Structure	Macrohabitat Geometry
Mesohabitat Structure	Mesohabitat Geometry, Cover
Monitoring, Capture, Handling	Scientific Study
Substrate Texture, Dynamics	Substrate Texture, Dynamics
Turbidity	Turbidity
Water Chemistry	Water Chemistry
Water Depth	Water Depth
Water Flow, Turbulence	Water Flow, Turbulence
Water Temperature	Water Temperature
Controlling factors	
Channel and Off-Channel Engineering	Channel and Off-Channel Engineering
FLSU Monitoring and Conservation Programs	(new)
Motorboat Activity	Motorboat Activity
Non-FLSU Fisheries	Fishing Activity and Fisheries Management
Nuisance Species Introduction and Management	Nuisance Species Introduction and Management
Tributary Inflows	Tributary Inflows
Wastewater and Other Contaminant Inflows	Wastewater and Other Contaminant Inflows
Water Storage-Delivery System Design and Operations	Water Storage/Delivery System Design and Operations

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ACKNOWLEDGMENTS

Becky Blasius, Jeffrey Lantow, and James Stolberg (LCR MSCP), and Robert Unnasch and Christine Wisnewski (Sound Science, LLC) provided invaluable feedback and guidance during preparation of this update. Brandon Albrecht (BIO-WEST, Inc.) provided welcome guidance on the recent findings for Lake Mead and the lower Grand Canyon.