



Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

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

2018 Updates

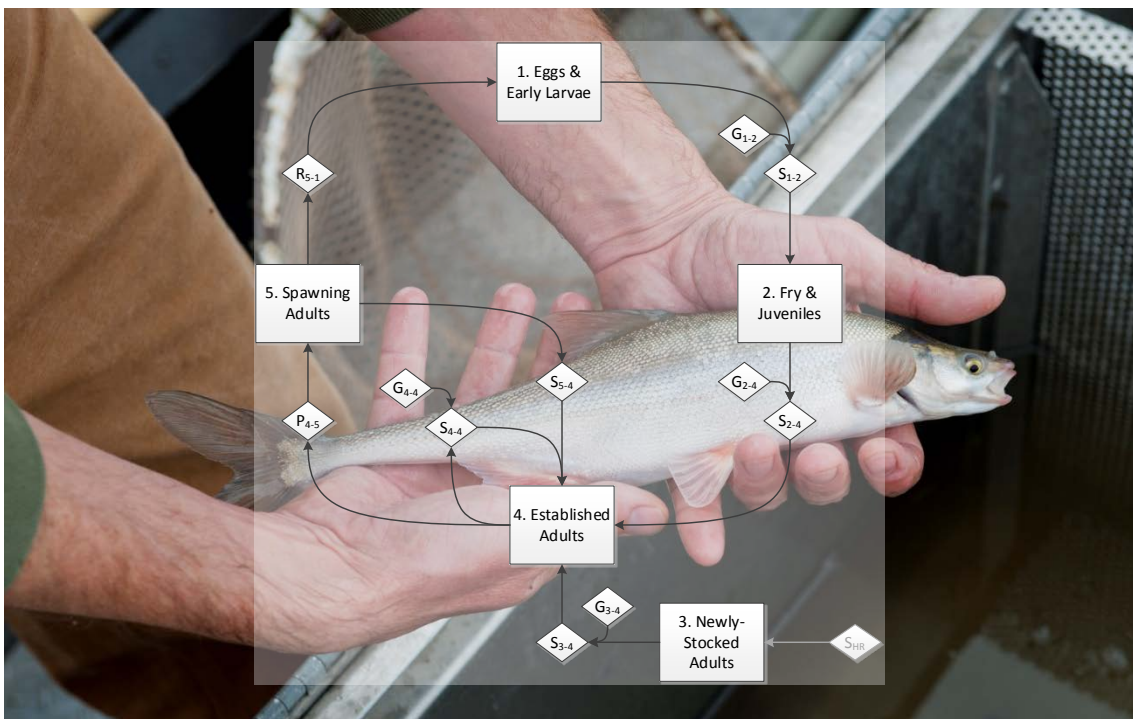


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March 2019

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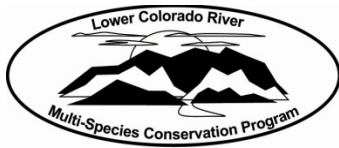
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Lower Colorado River Multi-Species Conservation Program

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

2018 Updates

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ACRONYMS AND ABBREVIATIONS

BONY	bonytail (<i>Gila elegans</i>)
ca.	circa (approximately, in reference to a date)
CAP	critical activity or process
CEM	conceptual ecological model
CF	controlling factor
CHLP	Cibola High Levee Pond
DNA	deoxyribonucleic acid
DO	dissolved oxygen
g	gram(s)
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
m	meter(s)
mg/L	milligram(s) per liter
mm	millimeter(s)
mtDNA	mitochondrial deoxyribonucleic acid
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 (<i>Xyrauchen texanus</i>)
Reclamation	Bureau of Reclamation
SL	standard length
TL	total length
UCRB	Upper Colorado River Basin
USDA	U.S. Department of Agriculture
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey
YOY	young of year

Symbols

°C	degrees Celsius (<i>aka</i> Centigrade)
≥	greater than or equal to
<	less than
%	percent

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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 bonytail (*Gila elegans*) (BONY) (Braun 2015). This update incorporates information reported in publications and presentations at professional meetings since the completion of the original BONY conceptual ecological model, and also incorporates information from the professional experiences of MSCP staff and other experts. An updated version of the CEM workbook incorporates the new information. This report is an appendix to the original CEM. The full CEM report, including its life-stage diagrams, has not been updated.

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

This update also provides a list of all literature cited in the updates to chapters 1–6. It provides a list of 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 new research and monitoring questions concerning gaps in knowledge that may bear on adaptive management of BONY. 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 decisionmaking 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

Bonytail (*Gila elegans*) (BONY) conservation efforts undertaken by the Lower Colorado River Multi-Species Conservation Program (LCR MSCP) along the lower Colorado River (LCR) ecosystem, and parallel recovery efforts in the Upper Colorado River Basin (UCRB) with BONY, continue to have poor results. Hatchery-reared BONY released into the LCR—other than those released into protected backwaters and isolated ponds—continue to disappear (no longer detected by passive integrated transponder [PIT] tag monitoring) within “the first several weeks to months post-release” (LCR MSCP 2017). One notable exception to this ongoing difficulty is the successful spawning of BONY in off-channel wetlands in the UCRB in 2015 and 2016 after stocking into the Green River.

BONY REPRODUCTIVE ECOLOGY

The discussion of BONY reproductive ecology in chapter 1 should be revised to provide updated information on the environment in which BONY evolved, spawning triggers and reproductive participation, and hybridization.

Update on BONY Reproductive Ecology: BONY Evolutionary Environment

As summarized by Minckley and Thorson (2007; see also Mueller and Marsh 2002), efforts to document the ecology of BONY began only after the species had already suffered massive declines in abundance and anthropogenic changes in the LCR ecosystem. As a result, little is known of BONY natural habitat preferences or the evolutionary ecology of the species – the environment and selective pressures that gave rise to the distinctive biological characteristics, behaviors, and habitat preferences of the species. Based on the weight of largely anecdotal information, Minckley and Thorson (2007) state, “These observations ... illustrate few collections from canyon bound reaches and increase where the river left the [Grand Canyon] entering the broad alluvial valleys downstream. This is where the meandering river formed a network of runs, pools, and braided channels, associated with backwaters that provided important nursery areas for native fish. It is here where the bonytail flourished, living in a relatively slow-moving river, punctuated by periods of massive floods and droughts, along shorelines scalloped with backwaters and stands of riparian vegetation.”

Recent reports help put these and other earlier reports in a stronger scientific context. BONY stocked in 2014–16 in two Lake Mohave backwater ponds — North Nine Mile and Nevada Egg ponds—readily spawned; BONY restocked into

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Cibola High Levee Pond (CHLP) regularly spawn; and BONY stocked in three ponds (Ponds 2, 5, and 6) at the Imperial Ponds Conservation Area (IPCA) in 2017 readily spawned in one of the ponds (Pond 2), as summarized by LCR MSCP (2017) and Osborne and Turner (2014, 2015, 2016, 2017). These reports point to the importance of low-velocity settings as BONY spawning habitat. Osborne and Turner (2017) specifically note from their studies of the Lake Mohave backwater ponds and IPCA Pond 2, “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 among both males and females may be higher in the backwaters than in lotic systems.”

The successful recruitment of BONY in off-channel wetlands in the UCRB in 2015 and 2016 (Bestgen et al. 2017) provides a new example of the importance of low-velocity settings not only as spawning habitat but also as nursery habitat. BONY stocked into the Green River spawned in off-channel wetlands, into which the stocked adults had to have moved prior to spawning, as indicated by the timing of spawning relative to the timing of connection of the wetlands to the river. In turn, the resulting larvae remained in the wetlands, with several individuals reaching juvenile (Age-0) size despite the presence of numerous predators. Bestgen et al. (2017) note that BONY spawn readily in off-channel wetlands, citing numerous previous reports documenting this along the LCR (e.g., Mueller 2006).

These recent findings reinforce the proposals of Mueller and Marsh (2002) and Minckley and Thorson (2007) concerning the core range and defining habitat for BONY. Mueller and Marsh (2002) note that, prior to major river regulation, both BONY and a second large native fish, the razorback sucker (*Xyrauchen texanus*) (RASU), were most common along the LCR rather than upstream. Further, they note that, prior to river regulation, neither BONY nor RASU were commonly captured in the main stem of the river, but were readily caught in backwaters, sloughs, lagoons, and other low-velocity environments off-channel, which often had lower levels of turbidity than the main channel. Such off-channel habitats were common historically across the Colorado River delta, from the Gila River confluence to the Gulf of California, as well as upstream, across the wide, highly braided wetted valley between the Gila River confluence and “Monument Canyon,” the present location of Parker Dam, and also across smaller braided reaches upstream between Monument Canyon and Grand Canyon (Mueller and Marsh 2002). Mueller and Marsh (2002) describe the pre-regulation delta as a “...vast maze of braided river channel, cottonwood, willow and mesquite forests, old oxbows, and cattail-margined sloughs.” Ohmart et al. (1988) provide additional details on the biology of the delta, including the abundant presence of

Typha and *Schoenoplectus*¹, based on Grinnell (1914), who in turn noted the high frequency of signs of muskrats and beavers throughout the abundant flood plain and deltaic habitats of the valley.

The recent findings on BONY spawning and habitat use also provide a context for better understanding the evidence that BONY thrived in prehistoric Lake Cahuilla. The Salton Basin of California, at the center of which today lies the Salton Sea, is the northern end of a depression that extends northward from the Gulf of California. The Salton Basin has filled with freshwater from the Colorado River several times over the past several thousand years, creating a waterbody known generally as Lake Cahuilla (or sometimes Lake La Conte) (Walker 1961; Waters 1983). The lake episodes resulted from changes in the course of the Colorado River to flow more directly westward from the Gila River confluence as well as simply from overflow and backflow from the Colorado River delta during floods. The present-day Salton Sea formed when the flooding Colorado River broke through artificial dikes in 1905–06 and directed its flow due westward into the Salton Basin (Walker 1961; Waters 1983).

The flooding of 1905–06 created only a small replica of prehistoric Lake Cahuilla, the ancient shoreline terraces of which indicate that it once reached depths up to 30 meters (m), with a length and width of approximately 180 and 50 kilometers (km), respectively, roughly six times the maximum area of the Salton Sea. The last major episode of Lake Cahuilla inundation began ca. A.D. 700 and continued into the late 1500s (Li 2003), during which the river continued to keep the lake full and overflowing to the south with only three to four brief interruptions during which the lake level fell due to evaporation without replenishment from the river. This last major episode of inundation followed multiple such episodes over the past 20,000 years and was followed by occasional minor episodes of partial filling prior to 1905 (Mueller and Marsh 2002).

The Colorado River floodwaters that created the Salton Sea carried in or provided an avenue for colonization by large numbers of fishes (Evermann 1916; Hurlbert et al. 2007), including probably every species present in the LCR in 1905–06. This assemblage included BONY and RASU, as well as common carp (*Cyprinus carpio*), striped mullet (*Mugil cephalus*), rainbow trout (*Oncorhynchus mykiss*), and catfish (Evermann 1916; Hurlbert et al. 2007). The same mechanism apparently introduced native fishes into Lake Cahuilla during at least its last major episode of inundation, ca. A.D. 700–late 1500s (see below), and presumably did so during prior major episodes of inundation as well.

¹ Three-corner or chairmaker's bulrush (*Schoenoplectus americanus*), California bulrush (*S. californicus*), and softstem bulrush (*S. tabernaemontani*), the three types of bulrush found along the LCR, were formerly classified in the genus *Scirpus* but are now assigned to the genus *Schoenoplectus*.

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As discussed in the original CEM report (Braun 2015), BONY skeletal remains are extremely abundant in archaeological sites in the Salton Basin dating ca. A.D. 700–late 1500s, indicating that BONY successfully colonized Lake Cahuilla during its last major episode of inundation. Gobalet et al. (2005) note that, among 4,869 fish remains recovered from archaeological sites in the Salton Basin and examined by them, “More than 98% of these ... identified to species are from razorback sucker (73.6%) and bonytail (24.9%).” The size distributions of the fish skeletal remains indicate that Native American exploitation of BONY and RASU from the lake probably focused mostly on spawning aggregations (Gobalet 1992; Gobalet and Wake 2000; Gobalet et al. 2005; White and Roth 2009). However, smaller individuals were also taken, and eaten whole, as indicated in coprolite remains (White and Roth 2009). The Native American exploitation of BONY and RASU resulted not only in substantial accumulations of bone remains but in the construction and maintenance of V-shaped fishing weirs – the numerous stone foundations of which are notable feature of the archaeological record in the basin (Gobalet 1992; Gobalet and Wake 2000; Gobalet et al. 2005; White and Roth 2009).

As discussed in chapter 4 (see “Aquatic Macrophytes”), Lake Cahuilla provided shallow to deep (up to 30 m) lacustrine habitat, with abundant shoreline marsh vegetation. The lake also would have presented turbid conditions due to circulation-generated turbulence and disturbance of shallow-water substrates, including sediment as well as mineral precipitates, with the latter forming as each lake episode evaporated (Walker 1961; Waters 1983; Li 2003). However, shoreline marsh waters around the lake would have been less turbid because marsh vegetation limits/inhibits turbulence and its resulting disturbance of fine substrates (see chapter 4, “Aquatic Macrophytes” and “Turbidity”). The shoreline marshes would have provided cover for BONY (see chapter 4, “Aquatic Macrophytes”). The Lake Cahuilla shorelines and shallows thus would have had many features in common with the backwaters, side channels, lagoons, and other off-channel habitats that were common throughout the Lower Colorado River Valley prior to river regulation. The fact that BONY apparently thrived in prehistoric Lake Cahuilla, at least episodically, thus further emphasizes the idea that the original core range of BONY lay in the backwaters and flood plain wetlands of the Colorado River and its delta below the present location of Parker Dam.

BONY water chemistry preferences and tolerances also reinforce this identification of the BONY core range. Given the opportunity to move among habitats, BONY tend to select water with high levels of total dissolved solids and can persist in water with a total dissolved solid concentration up to 4,700 milligrams per liter (mg/L) (Pimentel and Bulkley 1983). This is the highest tolerance for salinity reported for any *Gila* species in the Colorado River (LCR MSCP 2016). Similarly, the LCR MSCP (2017) has found that BONY eggs and larvae have higher tolerances (exhibit lower rates of mortality) at elevated salinity (measured as specific conductance) than do RASU eggs and

larvae. Unlike the rest of the Colorado River Basin, the prehistoric backwaters and flood plain wetlands of the LCR and its delta, and prehistoric Lake Cahuilla, would have sustained precisely such elevated salinities because they lay at the receiving end of the entire river basin and because the high evaporation rates in their lower desert climate would have further concentrated dissolved solids (Kniffen 1932; Walker 1961; Ohmart et al. 1988; Holdren and Montaña 2002; Li 2003; Hurlbert et al. 2007). The present-day salinity of the Salton Sea exceeds 4,400 mg/L (4.4 g/L), but it attained that concentration only after many decades of evaporative losses and inflows only of irrigation return flows with their own elevated salt concentrations (Walker 1961; Ohmart et al. 1988; Holdren and Montaña 2002; Li 2003; Hurlbert et al. 2007).

BONY also grow and reproduce best in warmer waters (see chapter 4, “Water Temperature,” in Braun [2015]). For example, juvenile and adult BONY have greater swimming strength and endurance in water above 20 degrees Celsius (°C) (see chapter 3, “Swimming”). Gorman and VanHoosen (2000) also found that BONY juveniles from rearing ponds were lethargic in cold (12 °C) water, but more active at 18 °C, and fully active throughout the water column at 24 °C; Pacey and Marsh (2008a) summarize reports that BONY exhibit very low metabolic rates at 15 °C. BONY avoid cold tailwaters created by hypolimnetic discharges from reservoirs (Minckley 1991; Clarkson and Childs 2000; Bestgen et al. 2008). Given a choice of water temperatures in which to position themselves in laboratory experiments, BONY prefer to locate themselves in water at 24.2 °C (Bulkley et al. 1982). BONY also tolerate fairly high water temperatures if allowed to acclimate: up to 37 °C after acclimation at 25 °C and up to 39 °C after acclimation at 30 °C (Carveth et al. 2006).

The prehistoric backwaters and flood plain wetlands of the LCR and its delta, including prehistoric Lake Cahuilla, would have presented a unique set of evolutionary challenges for BONY, and for RASU, with which they apparently shared this core range (Mueller and Marsh 2002; U.S. Fish and Wildlife Service [USFWS] 2002). As discussed in the original CEM (Braun 2015), BONY in this core range would have experienced both seasonal wetting and drying, and highly irregular, interannual variation in the magnitude, timing, and duration of wetting and drying, including episodes of drought and extreme flooding. Seasonal and interannual drying would have confined fishes to smaller and/or shallower and presumably more saline waters. As also discussed in the original CEM, BONY reproductive ecology can be understood as an adaptation to this challenging environment.

BONY also would have experienced selective evolutionary pressures from predation unique to this environment, as discussed below (see chapter 3, “Predation,” and chapter 4, “Aquatic Macrophytes,” “Aquatic Vertebrates,” and “Birds and Mammals”). For example, Mueller and Marsh (2002) note that BONY (and all other native fishes along the LCR) evolved alongside only a

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single aquatic predator, the Colorado pikeminnow (*Ptychocheilus lucius*). Consequently, they argue, BONY and other native fishes of the LCR would not have evolved complex repertoires of behaviors and physical adaptations in response to selective pressure from predation. Further, they argue that episodic droughts that knocked back native fish abundances in the LCR ecosystem would have differentially benefited BONY (and RASU), which can reproduce more rapidly and in greater numbers than the pikeminnow. This difference in reproductive ecology would have allowed BONY (and RASU) numbers to rebound quickly following droughts and reach reproductive size/age quickly, producing abundant cohorts of offspring to rebuild population numbers. At the same time, avian predation may have been particularly intense in marsh habitats, as discussed below (see chapter 3, “Predation,” and chapter 4, “Aquatic Macrophytes,” and “Birds and Mammals”).

Update on BONY Reproductive Ecology: Reproductive Participation and Fertility

The studies of spawning BONY in isolated backwater ponds, free of aquatic predators, around Lake Mohave in 2014–16 and at the IPCA in 2017 (see above; Osborne and Turner 2014, 2015, 2016, 2017) demonstrate that BONY have consistently high rates of reproductive participation, with 83 to 94% of all adults in each pond contributing to the production of offspring in any given year. Female participation rates are slightly lower than male rates, on average, within this overall range; however, the number of offspring produced by any one adult varies greatly. Analysis of the larvae produced by BONY spawning at IPCA Pond 2 in 2017, for example, indicated that the larvae resulted from 483 unique mate pairs, the majority of which produced only 1 offspring (Osborne and Turner 2017). Among these mate pairs, further, “The mean number of offspring per individual male and female was four but there was slightly more variance among contributing females.... Two females contributed at least 15 progeny each, whilst one male sired at least 12 progeny.”

Osborne and Turner (2014, 2015, 2016, 2017) also found that larger females (based on total length [TL] at stocking) tended to have more mates and produce more offspring; however, they did not see any such relationship among males. (The investigators also note that the stocked individuals exhibited a somewhat limited size range, because of their hatchery origin, and that they plan to investigate this possible relationship between size and fertility further with samples across a larger range of body sizes.) Condition data are not available for the BONY used in these studies of spawning in isolated ponds (Osborne 2018, personal communication).

Update on BONY Reproductive Ecology: Hybridization

A fully updated discussion of BONY reproductive ecology in chapter 1 would include information on hybridization as a natural phenomenon that has not eroded the distinctiveness of the species. However, the present interim update does not need to add this information to chapter 1. The inclusions of “Hybridization” as a new critical biological process and “Genetic Diversity” as a new habitat element, below, provide the necessary information for the present interim update.

Update on BONY Reproductive Ecology: Spawning Triggers

No significant new information has emerged on spawning triggers (see Bonar et al. 2011 for comments on triggers in other species in the genus *Gila*); however, recent findings and reconsideration of older information in light of these recent findings reinforce the understanding that BONY spawning may be triggered more by general seasonal patterns in temperature and photoperiod than by any specific thermal event(s), with flow conditions having little effect.

As noted above, BONY stocked in 2014–16 in two Lake Mohave backwater ponds—North Nine Mile and Nevada Egg ponds—readily spawned; BONY restocked into CHLP regularly spawn; and BONY stocked in IPCA Pond 2 in 2017 readily spawned, as summarized by LCR MSCP (2017) (see also Osborne and Turner 2014, 2015, 2016, 2017). None of these areas has a “natural” flow regime, and the water elevations at CHLP and the IPCA ponds are artificially controlled in ways that minimize variability. Further, the IPCA ponds are fed exclusively by groundwater wells (LCR MSCP 2017) and consequently have thermal regimes less affected by air temperatures than is the case in CHLP and especially in the Lake Mohave backwater ponds. CHLP and especially the Lake Mohave backwater ponds, in turn, also do not experience “natural” thermal regimes controlled by main stem flows.

The evidence discussed above concerning BONY abundance in prehistoric Lake Cahuilla also indicates that BONY do not require riverine flow conditions to spawn. The evidence from Lake Cahuilla is not new, but it can be better placed into context now, as more data accumulate for non-riverine spawning among BONY across the Lower Colorado River Basin.

This accumulating information concerning BONY spawning triggers does not change the accepted view that, despite occurring on different dates in different locations, BONY spawning events in the Lower Colorado River Basin (LCRB) AND UCRB all coincide with water temperatures in the range of 18–20 °C, per

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Mueller (2006). Ample evidence also indicates that BONY embryo survival is much greater at 20 °C than at lower temperatures (LCR MSCP 2016); consequently, one would expect BONY to spawn when water temperatures approach this range.

However, BONY in 2014–17 spawned in backwater and isolated ponds that lack natural water temperature regimes; therefore, it may be more accurate to say that BONY spawning is cued at least in part by a pattern of *seasonal change* in temperature and that the springtime pattern of change in photoperiod (increasing duration of daylight) may also play a role. Regulation of BONY behavior by photoperiod is also documented elsewhere in its life cycle: Sykes (2011) notes that BONY in hatcheries feed much less during winter, regardless of water temperature, indicating photoperiod control of this behavior. BONY can also control the effects of temperature on their behavior to some extent (e.g., by remaining in deeper, presumably cooler water during summer daylight hours [USFWS 2002; LCR MSCP 2016, 2017]), and by spawning at night, as documented by Mueller et al. (2003a) at CHLP. Mueller and Marsh (2002) previously had noted, “In Lake Mohave, spawning adults prefer deeper habitats during the day and after dark congregate in schools along shore where they probably spawn over large cobble.”

The evolving picture of BONY spawning triggers, therefore, is one of flexibility, in which BONY spawning occurs in response to a combination of seasonal signals, and in which BONY also can control where they spawn and at what time of day in part to further optimize the thermal conditions in which they spawn. Such flexibility, in turn, is consistent with the characterization of the reproductive patterns of all native fishes of the Colorado River as “... adaptations to the harsh, unpredictable physical environment of Colorado River Basin rivers and streams” (Bezzlerides and Bestgen 2002).

CONCEPTUAL ECOLOGICAL MODEL PURPOSES

The present 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. This will not be updated for the existing CEMs.

Updates to Chapter 2 – BONY Life Stage Model

EVIDENCE FOR BONY LIFE STAGES

This update does not include changes in the names or definitions of BONY life stages; however, it is important to note the continuing pattern of severe losses among BONY released into open environments such as Lake Mohave and Lake Havasu. Census data continue consistently to note high rates of loss among reared BONY upon release, with antenna contacting of PIT tags declining quickly and tapering out almost completely by roughly 12 weeks on average. The data also show little dispersion from the general vicinity of release areas (e.g., Karam et al. 2011, 2012, 2013; Humphrey et al. 2014, 2015, 2016; LCR MSCP 2017; McCall et al. 2017).

PROPOSED BONY LIFE STAGES

This update standardizes the names of the life-stage outcomes and adds a new set of outcomes focused on BONY growth. This has resulted in changes to table 1 and figure 1, the latter of which also appears in the cover page illustration.

Table 1.—BONY life stages in the LCR ecosystem

Life stage	Life-stage outcome(s)
1. Eggs and early larvae	<ul style="list-style-type: none">• Egg and early larval survival• Egg and early larval growth
2. Fry and juveniles	<ul style="list-style-type: none">• Fry and juvenile survival• Fry and juvenile growth
3. Newly stocked adults	<ul style="list-style-type: none">• Newly stocked adult survival• Newly stocked adult growth
4. Established adults	<ul style="list-style-type: none">• Established adult survival• Established adult growth• Established adult reproductive participation
5. Spawning adults	<ul style="list-style-type: none">• Spawning adult fertility• Spawning adult survival

This update to the BONY conceptual ecological model standardizes the names of BONY life-stage outcomes as follows: (1) “Survival Rate” is changed to “Survival” for all five life stages; (2) “Established Adult Reproductive Participation Rate” is changed to “Established Adult Reproductive Participation”; and (3) “Spawning Adult Fertility Rate” is changed to “Spawning Adult Fertility.”

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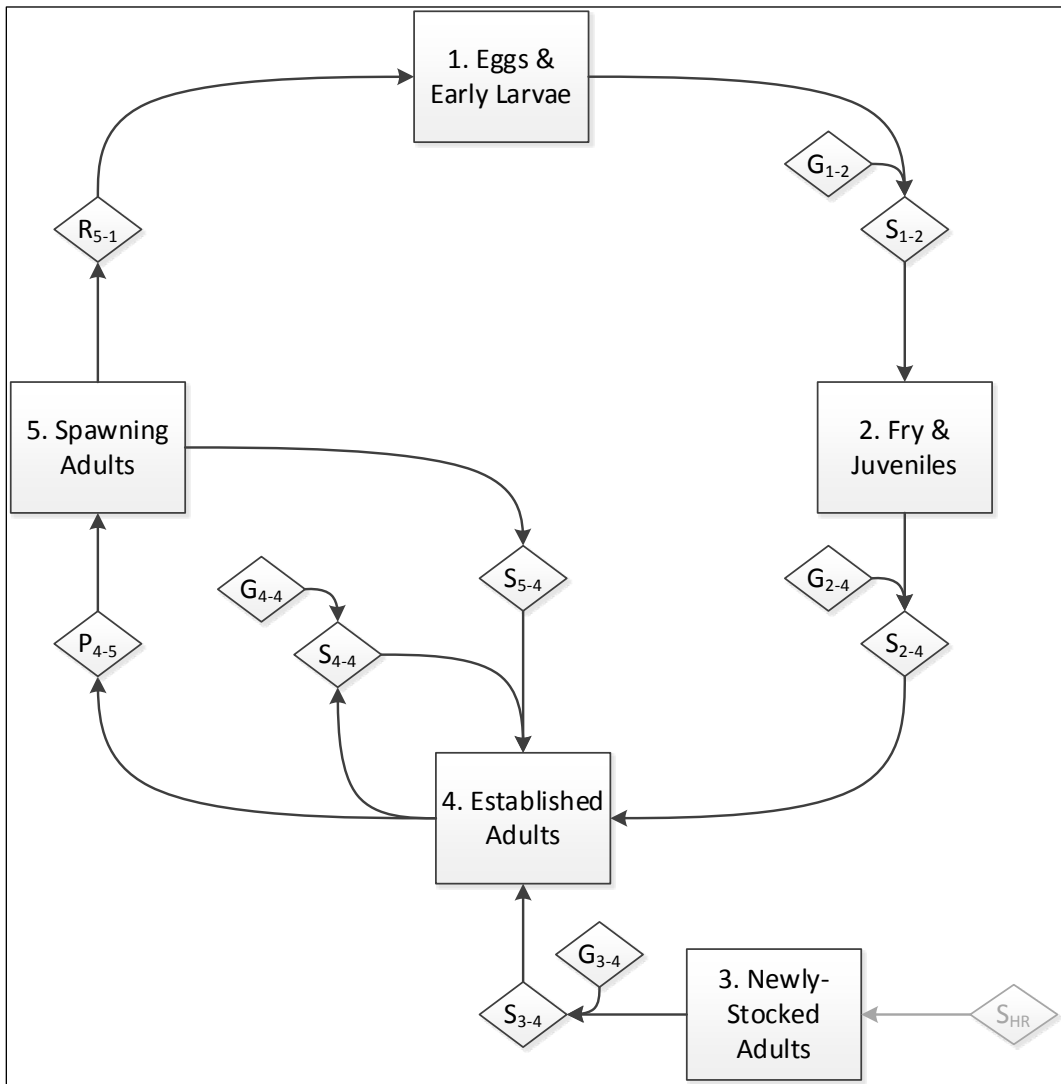


Figure 1.—Proposed BONY life history model.

Squares indicate the life stage, and diamonds indicate life-stage outcomes. Life-stage outcomes are rates, as follows:

S_{1-2} = survival, eggs and larvae; G_{1-2} = growth, eggs and larvae; S_{2-4} = survival, fry and juveniles; G_{2-4} = growth, fry and juveniles; S_{HR} = survival/output rate, hatchery programs (not fully assessed in conceptual model, but part of life cycle); S_{3-4} = survival, newly stocked adults; G_{3-4} = growth, newly stocked adults; S_{4-4} = annual survival, established adults in LCR habitat; G_{4-4} = annual growth, established adults in LCR habitat; P_{4-5} = participation of adults in spawning activity; S_{5-4} = survival, spawning adults; and R_{5-1} = fertility (reproductive output), spawning adults.

This update to the BONY conceptual ecological model adds “Egg and Early Larval Growth,” “Fry and Juvenile Growth,” “Newly Stocked Adult Growth,” and “Established Adult Growth” as life-stage outcomes for these four respective life stages. This change recognizes the importance of growth as an outcome parallel to survival. Growth includes egg maturation; increasing body size among larvae, juveniles, and adults (e.g., as measured by TL; maturation of morphology,

including various transformations in larval and juvenile morphology, and adult features such as the nuchal hump; 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), following episodes of stress and associated loss of body mass. The inclusion of growth as a life-stage 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 (*G. cypha*) (Yackulic et al. 2014) and brown trout (*Salmo trutta*) (Runge et al. 2018).

Numerous habitat elements affect BONY growth in each 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 CEM (Braun 2015). In turn, inhibited growth among BONY—as with inhibited growth in any fish species (Froese 2006; Hayes et al. 2017)—is likely to affect BONY critical biological activities and processes and other life-stage outcomes in several ways (Carveth et al. 2006; Bestgen et al. 2008; Gwinn 2011): Individual eggs, larvae, and juveniles 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 BONY adult vulnerability to predation depends, in part, on body size, as discussed in the original CEM, 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 larvae, juveniles, 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. 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 a life-stage outcome for growth among spawning adults. Spawning BONY, as with spawning individuals among fish species in general, presumably lose body mass as a result of their energy expenditures and, potentially, loss of appetite and/or diversion from foraging activity, during participation 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 life stage are simply adults in all other respects, and the CEM assumes that growth (gains or losses) 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 BONY. Osborne and Turner (2017) report for BONY “... a positive

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relationship between total length at stocking and the number of mates and offspring, such that larger females had more mates and offspring” but do not report on any relationships between Fulton’s condition factor (related to the mass-to-length ratio) and these demographic variables.

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) and Patiño et al. (2012) indicate that a variety of metal and synthetic organic compound contaminants are present in the Colorado River, tributary waters, and main stem impoundments, and in discharges to the river from urban areas and wastewater treatment outflows (see also Dwyer et al. 2005), and that these contaminants can bioaccumulate in the fish assemblage. However, the studies by Hinck et al. (2007) and Patiño et al. (2012) focused on abundant non-native fishes and did not examine any native fishes. Dwyer et al. (2005) separately determined that BONY are affected by such contamination, and their sensitivity to the contamination (e.g., lethal concentration levels), is roughly average among a range of tested native North American fishes. May and Walther (2013) present data on selenium in muscle tissue from one BONY caught in the Gunnison River, Colorado. The muscle sample contained selenium at a concentration significantly lower than that detected in other species in the same study; however, the authors provide no data on TL, age class, or indicators of fish health for the BONY examined, or for any other specimens, to assist in interpreting the results.

Gwinn (2011) examined growth and behavioral data on BONY exposed for 2.5 years to secondarily treated municipal wastewater, compared to BONY in a control environment. The municipal wastewater previously had been shown to contain low levels of known endocrine-disrupting compounds. Paretto (2007) previously had shown that BONY exposed to water from the same source for 3 months showed several signs of endocrine disruption, including feminizing effects in exposed males and androgenizing effects in exposed females (see also Walker et al. 2009). Gwinn (2011) found statistical evidence of some differences between the exposed and control fishes by the end of the 2.5-year experiment. The exposed BONY grew larger in both mass and length and achieved higher Fulton's condition factor scores, stayed out of cover more often when disturbed, dispersed more when outside of cover, and were more active than the control fishes. The study did not examine whether these effects would persist if the exposed BONY were placed into less-polluted water or whether these effects or those observed by Paretto (2007; see also Walker et al. 2009) could affect BONY survival, health, or reproduction.

This update accommodates some of this new information, and the addition of “growth” outcomes for most life stages, with the addition of links from Chemical Stress to Eggs and Early Larval Growth, Fry and Juvenile Growth, Newly

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Stocked Adult Growth, and Established Adult Growth. In turn, as discussed below (see “Foraging,” this chapter), the model adds links from these “growth” outcomes to survival for these four life stages and a link from Established Adult Growth to Established Adult Reproductive Participation. At the same time, the CEM retains direct links from chemical stress to survival and spawning reproduction because such stress can also affect these outcomes directly, separately from any effects it may have on growth.

COMPETITION

No change.

DISEASE

The discussion of this critical process is updated as follows:

Diseased BONY, as with diseased individuals among fish species in general, presumably lose body mass during illness as a result of their energy expenditures and, potentially, loss of appetite and/or diversion from foraging activity (Froese 2006; Nash et al. 2006). This update therefore includes causal links from disease to Egg and Early Larval Growth, Fry and Juvenile Growth, Newly Stocked Adult Growth, and Established Adult Growth. In turn, as discussed below (see “Foraging,” this chapter), the model adds links from these “growth” outcomes to survival for these four life stages, and a link from Established 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 reproduction, because disease can also affect these outcomes directly, separately from any effects it may have on growth.

DRIFTING

The discussion of this critical process is updated as follows:

The recent successful recruitment of BONY in off-channel wetlands in the UCRB (Bestgen et al. 2017) provides a new example of the importance of low-velocity settings not only as nursery habitat but as spawning habitat. Stocked BONY spawned in Green River off-channel wetlands, into which the stocked adults had to have moved prior to spawning, based on the timing of spawning relative to the timing of connection of the wetlands to the river. Larvae remained in the wetlands and grew to juvenile (Age-0) size despite the presence of numerous predators. Bestgen et al. (2017) note that BONY spawn readily in off-channel

wetlands, citing numerous previous reports documenting this along the LCR (e.g., Mueller 2006). Drifting would not be a significant factor in such settings because spawning sites would be located directly within potentially suitable nursery habitat. Drifting similarly is not a factor when BONY spawn near shorelines in ponds along the LCR and possibly would not have been a factor when they spawned in prehistoric Lake Cahuilla (see chapter 1, “BONY Reproductive Ecology”).

It should also be noted that for BONY larvae emerging from spawning sites in riverine settings, the currents in which they drift may not carry them exclusively downstream. Lateral and reverse currents, such as those that occur in eddies, can carry the drifting larvae between high- and low-velocity settings along their drift paths. The availability and distribution of such lateral and reverse currents depend on channel morphology (including channel geomorphic complexity) and hydraulics (Ryden 1999; Worthington et al. 2014). Channel sections along which lateral and reverse currents draw drifting larvae out of the main line of downstream flow into low-velocity settings such as shoreline embayments and entrances to backwaters may be termed “interception habitats”—a term developed for application to the drifting larvae of the endangered Pallid sturgeon (*Scaphirhynchus albus*) along the Missouri River (Jacobson et al. 2016). Kinzli and Myrick (2010) present a similar concept for the beneficial role of Rio Grande channel shoreline features in intercepting the drifting eggs of the Rio Grande silvery minnow (*Hybognathus amarus*) (see also Worthington et al. 2014). BONY larvae that emerge from spawning sites in riverine settings depend on the interplay of downstream and lateral drift, the availability of interception habitat, and their ability to swim between high- and low-velocity currents to move from their natal sites to nursery habitat. The latter consists of very low-velocity shoreline habitats, backwaters, embayments, tributary mouths, and flood plain marshes (see also chapters 1, 2, 4 and 6).

EGG SETTLING AND ADHESION

No change.

FORAGING

The discussion of this critical process is updated as follows:

BONY body condition presumably varies with foraging success for all motile life stages that forage (Froese 2006; Nash et al. 2006; Hayes et al. 2017). This update therefore includes a causal link from foraging to growth for all life stages for which a “growth” life-stage outcome has been added to the model. This

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change requires eliminating two types of links included in the original CEM (Braun 2015): (1) links from foraging directly to survival for those life stages that include foraging as a critical activity (i.e., for Fry and Juveniles, Newly Stocked Adults, and Established Adults) and (2) the link from Foraging to Reproductive Participation for Established Adults. These deleted links are replaced with links from Egg and Early Larval Growth, Fry and Juvenile Growth, Newly Stocked Adult Growth, and Established Adult Growth to survival for these four life stages and a link from Established Adult Growth to Established Adult Reproductive Participation.

HYBRIDIZATION

This critical biological process is a new addition to the CEM, defined as follows:

Hybridization occurs when two species together produce live offspring that share genetic materials from both parental species. Hybridization occurs commonly among freshwater fishes, and more commonly among *Cyprinidae*, which includes the genus *Gila*, than among any other family of freshwater fishes in North America (Scribner et al. 2001; see also Schönhuth et al. 2014). 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.” Their 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 LCR MSCP augmentation program for BONY relies on an extremely small initial broodstock of individuals captured from Lake Mohave between 1976 and 1981 (USFWS 2002; LCR MSCP 2006, 2015). The parents of the first generation raised in captivity consisted of five sires and six dams (Hamman 1982), but, as is typical of BONY (see chapter 1, “BONY Reproductive Ecology”), not all individuals actually participated in the initial captive spawning, resulting in an initial hatchery population descended from only eight individuals (Hedrick et al. 2000; Osborne and Turner 2016). Subsequent hatchery rearing relies on hormonal treatments to trigger gonadal development and manual expression of both male and female gametes (Osborne and Turner 2016) to eliminate BONY spawning variability as a limiting factor in reproduction. Nevertheless, concern with the limited genetic diversity of the BONY broodstock remains high. Efforts to expand the captive gene pool with additional wild individuals from Lake Mohave have failed (Minckley and Thorson 2007; Osborne and Turner 2016). Consequently, management of BONY along the LCR MSCP includes monitoring of the genetic diversity of the BONY broodstock, and any offspring

produced by BONY after release, to help ensure that management actions do not further compromise this diversity (LCR MSCP 2006, 2015, 2016, 2017; Osborne and Turner 2014, 2015, 2016, 2017).

Additionally, as summarized recently (LCR MSCP 2016):

As reviewed by the USFWS (2002), hybridization between bonytail and other native Colorado River Gila species appears to have been common. For example, within the Gila complex, inter- and intraspecific morphological variation is apparently extensive where bonytail, roundtail chubs, and humpback chubs occur sympatrically. The result of this apparently high degree of hybridization is a relatively high level of phenotypic plasticity, with multiple authors reporting multiple morphologic intergrades present in samples collected throughout the Colorado River (Holden 1968; Holden and Stalnaker 1970; Smith et al. 1979; Douglas et al. 1989, 1998; Kaeding et al. 1990). Such genetic intermixing was likely common historically and plausibly served to promote phenotypic plasticity and adaptability of the various species to their environment (Dowling and DeMarais 1993). Furthermore, Miller (1946) suggests evidence of species intergrades prior to anthropogenic influences. Recent mitochondrial- and allozyme-based deoxyribonucleic acid (DNA) research efforts suggest that bonytail are a uniquely adapted extension of the roundtail chub complex (Dowling and Demarais 1993). The extent of current and ongoing hybridization and its impacts on wild bonytail populations are unknown due to the absence of recent captures, but hybridization and its effects may become important as populations become established through hatchery introductions and overall species recovery, particularly as increasing populations of Gila become potentially and increasingly intermixed due to compressed habitat availability (USFWS 2002).

Hybridization between BONY and other *Gila* species therefore potentially could further compromise BONY genetic diversity. However, Gerber et al. (2001) present a counterpoint to this argument concerning hybridization between BONY and other *Gila* species in the Colorado River Basin. Specifically, Gerber et al. (2001) argue and provide supporting data that hybridizations involving BONY mostly appear to be instances of introgression in one direction only: BONY introgression with other *Gila* species, particular with the humpback chub, in the Lower Colorado River Basin, and with all morphological types in the UCRB. That is, Gerber et al. (2001) found that individuals in the LCRB morphologically identifiable as humpback chubs sometimes exhibited BONY mitochondrial DNA (mtDNA) haplotypes, but not vice versa. In the UCRB, individuals sometimes exhibited BONY mtDNA haplotypes regardless of which other *Gila* species their morphology indicated but, again, not vice versa.

Schönhuth et al. (2014; see also Page et al. 2017) similarly found that BONY are genetically distinct from the rest of the members of the genus *Gila* in the Colorado River Basin, based on mtDNA and other genetic indicators, with little or no introgression from any other Colorado River Basin *Gila* species. At the same time, Schönhuth et al. (2014) found consistent genetic support for a longstanding

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hypothesis that one of these other Colorado River Basin *Gila* species, the Virgin River chub (*G. seminuda*), is likely a hybrid of BONY and the roundtail chub (*G. robusta*). Schönhuth et al. (2014) also note that mtDNA variants may be evolutionarily neutral.

These findings suggest that hybridization does not pose a threat to BONY genetic integrity. Nevertheless, it is reasonable to include hybridization as a potential threat to the genetic diversity of BONY in the LCR ecosystem. The potential causes of hybridization among closely related fish species tabulated by Scribner et al. (2001) could all affect BONY in the LCR ecosystem if BONY were to come into contact with other closely related *Gila* species in the open system.

MECHANICAL STRESS

The discussion of this critical process is updated as follows:

BONY that experience mechanical stress, as with fish species in general, 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 (Froese 2006; Nash et al. 2006). This update therefore includes causal links from mechanical stress to Egg and Early Larval Growth, Fry and Juvenile Growth, Newly Stocked Adult Growth, and Established 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 Established 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 reproduction because mechanical stress can also affect these outcomes directly, separately from any effects it may have on growth.

PREDATION

The discussion of this critical process is updated as follows:

Predation continues to have a devastating effect on released BONY, resulting in a consistent pattern in antenna contacts with PIT-tagged BONY following release: Contacts decline quickly following release, tapering out almost completely by roughly 12 weeks on average, and also show little dispersion from the general vicinity of release areas (Karam et al. 2011, 2012, 2013; Humphrey et al. 2014, 2015, 2016; LCR MSCP 2017; McCall et al. 2017).

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

As discussed in chapter 1 (see “BONY Reproductive Ecology”), depredation by the Colorado pikeminnow may have been among the selective pressures shaping BONY reproductive biology. Mueller and Marsh (2002) argue that episodic droughts that knocked back native fish abundances in the LCR ecosystem would have selected for the ability of BONY to reproduce more rapidly and in greater numbers than can the pikeminnow. This difference in reproductive ecology would have allowed BONY numbers to rebound quickly following droughts and reach reproductive size/age quickly, 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, BONY and other native 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 influx of non-native aquatic predators. However, their suggestion overstates the case for the simplicity of the predatory environment prior to Euro-American impacts. Specifically, their suggestion does not recognize (1) the potential effects of natural predation on 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 shallow, low-velocity environments, such as those that seem particularly attractive and important to BONY along the Lower Colorado River Valley. Understanding BONY adaptations to predation therefore requires a consideration of what these adaptations might have looked like specifically in such shallow, low-velocity environments.

Information on avian predation along the LCR in fact has increased significantly in recent years and includes evidence from camera monitoring at Laughlin Lagoon, the Bill Williams River National Wildlife Refuge, and the IPCA, and field observations of avian predation and/or resulting talon and beak injuries to BONY in the Havasu National Wildlife Refuge and along Reaches 4–5 (Humphrey et al. 2014, 2015, 2016; Best 2015; Best et al. 2017; Lantow 2017; LCR MSCP 2017; McCall et al. 2017; Mueller 2017). Avian predation could account for mortality among a large fraction of released BONY.

Monitoring of post-release BONY along the LCR, in CHLP, and in the IPCA ponds show that released BONY mostly use deeper water during daylight and use

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near-surface waters and shorelines more at night (Marsh and Mueller 1999; USFWS 2002; Mueller et al. 2003a; Mueller 2006; Karam et al. 2012, 2013; Marsh et al. 2013a; Humphrey et al. 2014, 2016; LCR MSCP 2016, 2017). However, this is not a rigid pattern; Mueller (2006) also reports instances of BONY daytime aggregation near the water surface at CHLP. The monitoring of post-release BONY along the LCR, in CHLP, and in the IPCA ponds also has found that BONY seek cover in bulrush (*Schoenoplectus*), and sometimes also cattails (*Typha* spp.) (Karam et al. 2011, 2012, 2013; Humphrey et al. 2014, 2016), and disperse less in more turbid environments (LCR MSCP 2016). Field investigators also report difficulties detecting electronic tags on fishes that enter stands of emergent vegetation (Humphrey et al. 2014, 2016). As discussed in chapter 1 (see “BONY Reproductive Ecology”), prehistoric Lake Cahuilla would have provided plentiful opportunities for such diurnal movements and use of marsh vegetation cover as well.

Recent findings thus reinforce and clarify earlier findings that BONY prefer off-channel and other relatively shallow and/or low-velocity settings when given the choice, generally use shallower waters within these settings mostly at night, and use both turbidity and habitat structure as cover. Such habitat structure can include crevices in substrates, overhanging banks and vegetation, large woody debris, and emergent aquatic vegetation, with bulrush (*Schoenoplectus* spp.) vegetation a commonly used cover type (e.g., Minckley 1991; USFWS 2002; Mueller 2006; Karam et al. 2012, 2013; Marsh et al. 2013a; Humphrey et al. 2014, 2016; Mueller et al. 2014; LCR MSCP 2017), as noted above. Mueller (2006) also notes that the dark dorsal surface of adult BONY bodies contrasts with lighter substrates in shallow waters, making it easier for predatory birds, such as great blue herons (*Ardea herodias*) to detect and prey on them. By implication, however, such body coloring presumably would make BONY less detectable from above when they swim above dark substrates.

The pre-regulation backwaters and flood plain wetlands of the LCR and its delta sustained very large numbers of resident and migratory waterfowl (Ohmart et al. 1988). Prehistoric Lake Cahuilla likely also sustained a similar abundance of waterfowl: Bones from archaeological sites (Gobalet 1992; Gobalet and Wake 2000; Gobalet et al. 2005) and historic data following the formation of the Salton Sea (Grinnell 1914; Patten et al. 2003; Hurlbert et al. 2007; Riedel et al. 2007) indicate intensive use of the waterbody and its shoreline marshes by migratory waterfowl, including numerous species now known or suspected to prey heavily on BONY, as discussed in chapter 4 (“Birds and Mammals”).

How were BONY (and RASU) able to thrive in Lake Cahuilla despite the abundance of avian predators? The recent and ongoing direct studies of avian predation on fishes along the LCR (e.g., Best 2015; Best et al. 2017; Mueller 2017; see chapter 4, “Birds and Mammals”) indicate that avian predators kill and eat essentially any fishes they can see in the clear modern waters. Two BONY behaviors described above may be hypothesized to have evolved under this

selective pressure: (1) BONY avoid near-surface waters during daylight hours (USFWS 2002; LCR MSCP 2016, 2017) and (2) BONY use emergent aquatic vegetation and turbidity as cover (see chapter 4, “Aquatic Macrophytes” and “Turbidity”). The near-shore shallows of the lake apparently had extensive cattail (*Typha*) and bulrush (*Schoenoplectus*) marsh vegetation, as indicated in coprolite and pollen data from archaeological sites (Wilke et al. 1977). The presence of remains of these genera in archaeological sites arises because both plant groups were heavily exploited for food and technologies (Wilke et al. 1977).

Riedel et al. (2007) also note that fish size and shape affected avian predation among fish-eating birds around the present-day Salton Sea. The present-day fish assemblage in the sea does not include any fishes native to the Colorado River. However, the pattern detected by Riedel et al. (2007) appears to relate to general properties of fish size and shape rather than to the palatability of particular fishes to particular birds. Specifically:

Tilapia (*Oreochromis mossambicus* x *O. urolepis hornorum*) is the most important resource for fish-eating birds. *Tilapia* grow fast to a size that is readily handled by large birds and are the most abundant fish in the lake. *Bairdiella* (*Bairdiella icistia*) grow to a smaller size over a longer period. *Corvina* (*Cynoscion xanthulus*), sargo (*Anisotremus davidsoni*), and shad (*Dorosoma cepedianum*) are less important for fish-eating birds because they quickly grow to sizes outside bird handling capabilities (*corvina*) or are not readily catchable and currently of low abundance (*shad* and *sargo*). Shape, in particular girth, determines the weight of the largest individual fish that a bird can handle; a slender 1,000 g *corvina*, for example, being more easily ingested than a deeper-bodied 1,000 g *tilapia*.

BONY of all age classes have a body form that is more slender than that of *corvina*. RASU, on the other hand, have a body form that is even more deep-bodied than that of *tilapia*, including a nuchal hump that develops as RASU mature (Minckley et al. 1991). As noted above, both BONY and RASU mature quickly into adults. BONY and RASU body forms and growth rates thus presumably affect their vulnerability to avian predation.

Finally, as noted in chapter 1 (see “BONY Reproductive Ecology”), BONY adult vulnerability to predation may depend in part on body size, as discussed in the original CEM (Braun 2015). Bestgen et al. (2017) note, “The effects of [BONY] size at stocking into the upper Colorado River are the focus of ongoing analyses, as larger fish may survive at higher rates (Badame and Hudson 2003; Nesler et al. 2003; Zelasko et al. 2010).” However, the intensity of any such relationship is not presently known, and the effects of BONY size on survival, among released BONY, is not currently a topic of investigation (LCR MSCP 2017). 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 BONY

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have a slender body form. Further, unlike some other native fishes of the Colorado River Basin, BONY develop only a slight dorsal keel as adults (USFWS 2002), which would have only mildly discouraged pikeminnow predation and only among BONY longer than 200 millimeters (mm) TL (Portz and Tyus 2004; Franssen et al. 2007).

Body 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 larvae, juveniles, 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.

RESTING/HIDING

This critical activity formerly named simply “Resting” 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. Fishes may “rest” merely by moving to/staying in locations where they can hold their position without significant expenditures of effort; however, they may also do so in habitat settings that provide cover to hide themselves from predators and/or secure themselves against hydrologic disturbances that could otherwise displace them. As noted above, increasing evidence indicates that BONY use crevices in substrates; overhanging banks and vegetation; large woody debris; and emergent aquatic vegetation, with bulrush (*Schoenoplectus* spp.) a commonly used cover type; turbid waters; and depth itself as protective habitat for resting/hiding. They also tend to rest/hide in deeper waters during daylight.

This update also notes that BONY resting/hiding behavior in all motile life stages potentially may 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 in water with high versus low turbidity (see chapter 4, “Turbidity”). For example, as noted below (see chapter 4, “Monitoring, Capture, Handling”), BONY use of dense aquatic macrophyte stands as cover can interfere with efforts to track—i.e., to telemetrically contact—individuals released with electronic tag implants that move into such habitat (Karam et al. 2013; Humphrey et al. 2014, 2016; Best et al. 2017). The likelihood of capture by different methods (e.g., by electrofishing or various net-based methods) similarly may vary in relation to these same factors (again, see chapter 4, “Monitoring, Capture, Handling”). These relationships are suggested based on studies of other native fishes in the Colorado River, including the closely related humpback chub (Bestgen et al.

2007; Rogers et al. 2008; Stone 2010; Van Haverbeke et al. 2013; Yackulic et al. 2018). Conversely, efforts to capture fishes may cause them to flee toward cover (again, see chapter 4, “Monitoring, Capture, Handling”), resulting in a bi-directional relationship.

SWIMMING

The discussion of this critical process is updated as follows:

Mueller and Marsh (2002) note for BONY, “The streamlined body suggests the fish is adapted to swift currents; however, studies suggest they prefer eddies and pools. This might help explain their success in reservoirs.” This statement may need refinement, given the growing evidence that the core range that shaped BONY evolution consisted of the backwaters and flood plain wetlands of the LCR and its delta. Swift currents may have been settings that BONY mostly passed through.

Moran et al. (2016) examined the possible specialization of BONY tail skeletal morphology and musculature for high swimming speeds by comparing these properties among four species: BONY, “... roundtail chub (*Gila robusta*), a closely related species from low-flow habitats; the common carp, an invasive cyprinid also found in low-flow habitats; and the chub mackerel (*Scomber japonicus*), a model high-performance swimmer from the marine environment.” The results indicate that BONY have several tail skeletal features similar to those of the chub mackerel that give it a more streamlined body than exhibited by the roundtail chub or the common carp. However, BONY tail morphology is not as streamlined as seen in the chub mackerel, and the chub mackerel has a significantly higher proportion of red muscle than seen in the other three species, which closely resemble each other in this respect.

The abstract for the paper by Moran et al. (2016) somewhat inaccurately asserts that the results indicate BONY tail morphology and musculature evolved in response to “...the selection pressures of the historically fast-flowing Colorado River, where flooding events and base flows may have required native species to produce and sustain very high swimming speeds to prevent being washed downstream.” However, the body of the article more accurately states that the results indicate, “Although *G. elegans* and *S. japonicas* share numerous morphological locomotor specializations, *G. elegans* may ultimately be limited in its sustained swimming performance by the lack of fatigue-resistant musculature. ... As a result, *G. elegans* may have a reduced [relative] ability to swim steadily for long periods of time at very high water velocities. ... When compared to the relatively homogeneous habitat of the scombrids, the Colorado River is a complex environment made up of turbulent runs and low flow pools. *G. elegans* may rely

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on short periods of burst swimming ... while maintaining position or moving.” Moran et al. (2016) do not also mention the ability of BONY to leap out of the water to escape capture (Mueller 2006), an example of burst-like behavior consistent with the findings concerning tail skeletal morphology and musculature. Such leaping behavior may be adaptive not only for escaping aquatic predators but for moving past obstacles that might occur in low-velocity settings with woody debris and dense aquatic vegetation – but not for escaping avian predators.

Chandos (2017) examined the effects of temperature on the swimming performance of juvenile bonytail, humpback chub, and roundtail chub acclimated to specific test temperatures (10 °C, 16 °C, 20 °C, or 30 °C) for 7 days. Results indicate that BONY have a higher average value for U_{crit} than do either of the other species when U_{crit} is measured in absolute units of $cm \cdot s^{-1}$ rather than in relative units of body lengths per second, have higher absolute U_{crit} values at temperatures ≥ 20 °C, and exhibit increasing absolute U_{crit} values with increasing body size. The assessment of body size used standard length (SL) and classified the test BONY into three classes: small (n = 32, 47–67 mm SL), medium (n = 32, 92–110 mm SL) and large (n = 3, 132–168 mm SL).

The evidence from the studies by Chandos (2017) and Moran et al. (2016), together with the basic concepts underlying the use of Fulton’s condition factor (Froese 2006; Nash et al. 2006), suggest that BONY swimming performance likely varies with body condition. The CEM recognizes this as a possible causal relationship for all life stages for which a “growth” outcome has been included in this update.

The increased information about avian predation on BONY (see “Predation,” this chapter) also brings into clearer light an older statement by Montony (2008) that BONY show fright response to birds overhead, indicating reactivity to avian predators. This presents another example of BONY possessing an innate repertoire of behaviors shaped by selective pressure from predation.

It should be noted that the BONY conceptual ecological model—both the original (Braun 2015) and this update—treats the swimming activities associated with spawning simply under “Swimming” for the Spawning life stage rather than as a separate critical process. The RASU model includes a separate “Staging/Spawning” process for this life stage because spawning RASU exhibit distinctive staging behaviors that warrant recognition. Spawning BONY do not exhibit distinctive staging behaviors.

THERMAL STRESS

The discussion of this critical process is updated as follows:

The evidence presented by Chandos (2017) (see “Swimming,” this chapter) indicates that BONY swimming performance varies with water temperature. Altered water temperatures could alter BONY swimming performance, although acclimation may reduce the severity of effect.

The addition of “growth” life-stage outcomes makes it possible for the CEM now to distinguish chronic thermal stress, which impairs activity levels, performance, and growth, from acute stress that may also impair activity levels and performance but also have even more dire effects. This will involve adding links from Thermal Stress to the “growth” outcome for those life stages for which this update includes a “growth” outcome, based on the basic concepts underlying the use of Fulton’s condition factor (Froese 2006; Nash et al. 2006).

Updates to Chapter 4 – Habitat Elements

AQUATIC MACROPHYTES

The definition and discussion of this habitat element is 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 Ohmart et al. (1988), Mueller (2006, 2007), Fernandez and Madsen (2013), Marsh et al. (2013a), the U.S. Department of Agriculture’s (USDA) PLANTS Database (USDA 2016), and the National Invasive Species Information Center (NISIC) (2017). The species listed in table 2 and the detritus from them may provide cover and food for BONY; habitat, including periphyton foods, for aquatic and terrestrial invertebrates that BONY may consume; and habitat for aquatic invertebrates, aquatic vertebrates, and birds that may prey on or compete with BONY (see chapter 3, “Competition,” “Foraging,” “Predation,” and “Resting/ Hiding”).

Aquatic macrophytes also reduce turbidity within their stands by reducing water flow velocities and turbulence, which allows suspended solids to settle to the substrate (Kadlec and Knight 1996; Mitsch et al. 2005; Faber-Langendoen et al. 2008). Prolonged elevated turbidity reciprocally may affect aquatic macrophyte recruitment. On the other hand, extremely high densities of macrophytes presumably also could exclude BONY, and potentially could limit light penetration to the water surface and water circulation, thereby affecting dissolved oxygen (DO) concentrations and possibly other aspects of water chemistry (Finnegan 2013; NISIC 2017). As noted in chapter 3 (see “Predation”), field investigators along the LCR also report difficulties detecting electronic tags on fishes that enter stands of aquatic macrophytes (Humphrey et al. 2014, 2016).

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 (Ohmart et al. 1988; Johnson 1991). Aquatic macrophytes in these settings, in fact, may have helped sustain their own habitat by stabilizing substrates and slowing the movement of water (Carlson et al. 1979; Fernandez and Madsen 2013).

The aquatic macrophyte assemblage along the LCR and its backwaters has changed as a result of river regulation and introductions of non-native plant species. Shallow backwaters, embayments, and tributary confluences continue to

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Table 2.—Aquatic macrophytes of the LCR

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

¹ Key: I = introduced, N = native, and ? = disputed.

² Species formerly classified as genus *Scirpus*.

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 2017). Fortunately, control efforts appear to be effective (Thorson et al. 2014). One or more possibly non-native varieties of common reed (*Phragmites australis*) (Saltonstall 2002) also may occur, contributing to the spread of common reed throughout the LCR ecosystem.

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 2016). Narrowleaf and hybrid cattails have similar habitat requirements and can grow in deeper water compared to broadleaf cattails (Motivans and Apfelbaum 1987). Both narrowleaf and hybrid cattails aggressively out-compete broadleaf and southern cattails for habitat, not only by occupying deeper waters but by establishing themselves in dense, 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 they can reproduce asexually from their rhizomes, forming clones that can spread up to 8 meters (m) per year (Pennsylvania Department of Conservation and Natural Resources [PADCNR] 2016). Aggressive expansion is more likely in disturbed wetlands, and hybridization exacerbates this potential. Triggering disturbances may include changes in hydrology, wildfire suppression, or nutrient enrichment (Wilcox et al. 1984)—common risk factors across the LCR ecosystem.

The USDA PLANTS Database (USDA 2016) currently does not include any occurrences of hybrid cattails within the LCR ecosystem; however, this apparent absence may only reflect a pattern of misidentification resulting from the lack of systematic attention to the taxonomy of cattails along the LCR and difficulties in distinguishing between narrowleaf and hybrid cattails 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 2017), and may provide less cover habitat for larger BONY. 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).

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Table 2 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 m long (National Research Council [NRC] 1991; Kennedy and Gloss 2005). As a result, it can have ecological effects similar to true macrophytes. This type of algae is more common in the Colorado River main stem upstream of the LCR, such as in the Grand Canyon, and requires clear water, but it can occur along the LCR (Ruiz 1994). It colonizes all substrate types, from soft and fine to coarse and hard (Stevens et al. 1997).

AQUATIC VERTEBRATES

The definition and discussion of this habitat element is 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 BONY or its habitat along the LCR, its connected backwaters, and its isolated ponds. Interactions may include predation on, competition with, or serving as food items for BONY. Most of these vertebrates are native and non-native fishes. Activity levels may vary in response to other habitat conditions (e.g., water temperature and water quality).

Table 3, updated, lists all aquatic vertebrates reported in the present-day LCR (Ohmart et al. 1988; Minckley 1991; Mueller and Marsh 2002; Minckley et al. 2003; Gloss and Coggins 2005; Marsh and Pacey 2005; Nonindigenous Aquatic Species Program 2017; Pool et al. 2010). Table 3 mostly lists fishes, but it also lists 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 (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 BONY do not have access to the latter but 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 2017). Table 3 also indicates which aquatic vertebrate species the literature explicitly reports or proposes in any life stage as a predator on BONY in both the lower and upper Colorado River (see chapter 3, “Predation”).

Updates to Chapter 4 – Habitat Elements

Table 3.—Aquatic freshwater vertebrates of the LCR

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

¹ B = introduced bait or forage fish, N = native, and S = introduced sport fishes.

² Is species known to prey on BONY?

³ Do juveniles (J) or adults (A) of the species compete with BONY for food or habitat?

“X” = reported in LCR literature, and “?” = suggested by species data in Froese and Pauly (2018), NatureServe Explorer (NatureServe 2018), or the U.S. Geological Survey’s Nonindigenous Aquatic Species Program (<http://nas.er.usgs.gov/default.aspx>).

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The literature reporting or proposing individual aquatic vertebrate species as a predator on BONY in the LCRB includes Bozek et al. (1984), Mueller and Marsh (2002), Mueller (2006, 2007), Mueller et al. (2006), Karam and Marsh (2010), Karam et al. (2011, 2012, 2013), Humphrey et al. (2014, 2015, 2016), and McCall et al. (2017). The parallel literature for the UCRB includes Joseph et al. (1977), Christopherson et al. (2004), Brunson and Christopherson (2005), Bestgen et al. (2008, 2017).

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

The large number of entries in table 3 for possible competition reflects the fact that BONY are omnivorous (see chapter 3, “Foraging”). This puts them in potential competition with numerous aquatic omnivores, herbivores, insectivores, crustaceans, 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 BONY or its habitat along the LCR and its connected backwaters. This range includes species known or potentially able to prey on BONY 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 strongly suspected to prey on BONY along the LCR. The list now includes great blue herons, kingfishers (*Megaceryle alcyon*), osprey (*Pandion haliaetus*), American white pelicans (*Pelecanus erythrorhynchos* and possibly other *Pelecanus* spp.), double-crested cormorants (*Phalacrocorax auritus*), and possibly other *Phalacrocorax* spp. (Mueller 2006; Kesner et al. 2008; Humphrey et al. 2014, 2015, 2016; Best 2015; Best et al. 2017; Lantow 2017; LCR MSCP 2017; McCall et al. 2017; Mueller 2017). Humphrey et al. (2016) also report turkey vultures (*Cathartes aura*) roosting in the vicinity of BONY habitat in the

Bill Williams River National Wildlife Refuge, and Best et al. (2017) also identify 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*) visiting or roosting at Laughlin Lagoon during periods when BONY were present.

Knowledge about the ecology of avian predation on BONY has increased particularly through the work of Best et al. (2017) and Mueller (2017) at Laughlin Lagoon and the LCR MSCP at the IPCA, where BONY were restocked in Ponds 2, 5, and 6 in February 2017 (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 combined photographic arrays on perching/roosting poles and antenna arrays to detect PIT tags from tagged RASU and BONY consumed by predatory birds using the poles during winter 2015, spring 2016, and winter 2016. The RASU and BONY were deliberately stocked into the lagoon for purposes of the study. The results indicated significant predation on both fish species by double-crested cormorants, with additional but much lower rates of predation by great blue herons and osprey. Further, the birds consumed RASU and BONY 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, and 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 observed more cormorant activity after 12 months. This increased activity typically consists of two to four birds feeding primarily in Pond 2, where a large spawn of BONY in 2017 resulted in "lots of small fish in the pond" (Lantow 2017, personal communication). LCR MSCP biologists also observed great blue herons in the area prior to the BONY stocking, "presumably feeding on mosquito fish in the drainage ditch or Pond 5" (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.

The study of avian predation on fishes around the Salton Sea by Riedel et al. (2007) may also provide relevant information on the possible dynamics of avian predation on BONY and other fishes native to the LCR, as discussed in chapter 3 (see "Predation"). Much literature exists on the ecology and management of avian piscivory (e.g., Cezilly 1992; Cowx 2003; Steinmetz et al. 2003; Beckmann et al. 2006; Wiese et al. 2008). Much of this literature focuses on commercial

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fisheries and aquaculture but nonetheless presents information potentially relevant to the problems posed by avian piscivory on BONY and other 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 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. 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 has not similarly evolved. The main source of information on this topic remains Mueller (2006), which reports observations of, and reasons for suspecting mammalian predation on RASU at CHLP 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.

On the other hand, at least two mammals may affect BONY 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, including its delta, and once helped create mesohabitat conditions beneficial to BONY by introducing woody debris and creating marshes and pools along backwater channels (Grinnell 1914; Kniffen 1932; Minckley and Rinne 1985; Ohmart et al. 1988; Stevens et al. 1997; Yohe II 1998). Both species are still present (Boutwell 2002; Hautzinger 2010; 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 shape their availability and generate particulate organic matter (POM) at the same time (Henker 2009), affecting food availability and physical habitat for BONY.

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

BONY vulnerability to avian and mammalian predation may also depend on turbidity, and the availability of vegetative cover (Humphrey et al. 2016; see

“Aquatic Macrophytes,” and “Turbidity,” this chapter). Other factors that may affect BONY vulnerability to avian and mammalian predation include BONY seasonal movement to nearshore shallows for spawning (see chapter 1, “BONY Reproductive Ecology”), and hatchery conditioning to aggregate near the water surface (see “Pre-Release Conditioning,” this chapter).

The evidence for BONY abundance in prehistoric Lake Cahuilla also offers a possible window into the ecology of avian predation on BONY. As noted above (see chapter 3, “Predation”), bones from archaeological sites around the shorelines of Lake Cahuilla (Gobalet 1992; Gobalet and Wake 2000; Gobalet et al. 2005) and historic data from the Salton Sea (Grinnell 1914; Patten et al. 2003) indicate intensive use of the waterbody and its shoreline marshes by large numbers of migratory waterfowl. These waterfowl include all of the species known or strongly suspected to prey on BONY along the LCR, as listed above, as well as many other potentially piscivorous birds. As also noted above (see chapter 3, “Predation”), this pattern suggests that BONY likely evolved under essentially constant ecological and evolutionary pressure from avian predation. BONY 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 “Aquatic Macrophytes,” this chapter), could have evolved at least partially in response to such pressure, as may some aspects of BONY skeletal structure, musculature, and swimming behaviors (see chapter 3, “Predation”).

FISHING ENCOUNTERS

No change.

GENETIC DIVERSITY

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

Full name: The genetic diversity of BONY individuals. This element refers to the genetic homogeneity versus heterogeneity of the BONY population during each life stage, both overall and within individual sites of rearing and release. As noted elsewhere in this CEM (see chapter 3, “Hybridization”), the LCR MSCP operates an intensive program of rearing BONY from a limited broodstock in off-site facilities for later experimental treatments and release into Lake Mohave, Lake Havasu, and below Parker Dam, and into CHLP, the IPCA, and other isolated ponds (see chapter 5, “BONY Monitoring and Conservation Programs”). The BONY from this rearing program released into these settings, and their offspring, are thought to constitute 100% of the individuals present in the LCR ecosystem (i.e, no wild BONY are thought to be present). The LCR MSCP

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augmentation program therefore is the dominant driver of genetic diversity among BONY in the LCR ecosystem. Selective pressures on released BONY (e.g., from predation) are thought to have no effect on subsequent generations in the LCR ecosystem because released BONY do not appear to survive long enough to spawn outside of isolated ponds such as CHLP or at the IPCA.

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 (USFWS 2002; Minckley et al. 2003; LCR MSCP 2006, 2015, 2016, 2017; Osborne and Turner 2014, 2015, 2016, 2017). As discussed elsewhere (see chapter 3, “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.

INFECTIOUS AGENTS

No change.

INVERTEBRATES AND PARTICULATE ORGANIC MATTER

The following paragraph is added to the end of the definition of this habitat element:

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

MACROHABITAT STRUCTURE

This habitat element replaces the original “Macrohabitat Geometry,” with a slightly updated definition 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 investigators working in the basin apply the term “macrohabitat” to both scales (e.g., Holden 1999; Budy et al. 2009). Examples of macrohabitat types, as defined in the present CEM, include the main channel, islands, side channels, tributary mouths, sloughs, bays, disconnected backwaters, 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 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.

Scattered historic (Holden 1973; Holden and Stalnaker 1975; Smith et al. 1979; Bozek et al. 1984; Kaeding et al. 1986; Minckley 1991; Marsh and Mueller 1999; Mueller and Marsh 2002; USFWS 2002; Christopherson et al. 2004; Brunson and Christopherson 2005; Modde and Haines 2005; Bestgen et al. 2006, 2007, 2008; Mueller 2006, 2007; Minckley and Thorson 2007; Pacey and Marsh 2008a; Valdez et al. 2011; Bottcher et al. 2013; Mueller et al. 2014; LCR MSCP 2016) and archaeological observations along the upper and lower Colorado River and its tributaries (see above) suggest that adult BONY occupied main stem and tributary river reaches in canyons, reaches with adjacent flood plain, and backwaters with depths < 10 m and low to moderate flow velocities, including the Colorado River Delta and Lake Cahuilla/Salton Sea (see chapter 1, “BONY Reproductive Ecology”) and spawned on shoals within these same macrohabitat types. Research continues to address the topic of BONY macrohabitat associations (LCR MSCP 2017).

MESOHABITAT STRUCTURE

This habitat element replaces the original “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 BONY 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 BONY use of these settings. Relevant variables that distinguish mesohabitats include depth; horizontal and vertical form, including hydraulic gradient; flow velocity, direction, and turbulence; substrate characteristics, including size, shape, and stability; aquatic vegetation types and density; range of variation in turbidity; and proximity to other mesohabitats.

Valdez et al. (2012a) refer to variables that distinguish mesohabitats as “microhabitat” characteristics. Each combination of conditions among these variables 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., Holden 1999; Budy et al. 2009) (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 BONY 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 referring to such settings as “interception habitat,” following terminology developed for a CEM for the endangered pallid sturgeon, to support species recovery along the Missouri River (Jacobson et al. 2016). However, the literature on mesohabitats and native fish ecology along the Colorado River does not yet use this term.

Scattered historic and recent observations along the upper and lower Colorado River, its tributaries, and isolated backwaters record the presence of BONY in a range of mesohabitats during different life stages and during different times of the day. However, few investigators gave close attention to BONY use of different mesohabitats prior to the historic collapse of the species across the UCRB and LCRB. In turn, BONY mesohabitat use today is rarely closely observed outside of artificial settings, although this situation is changing as the

scope of releases of BONY expands in both the UCRB and LCRB. As a result, the literature records only a handful of potential associations between particular BONY life stages and particular mesohabitat or cover types. The present CEM recognizes this pervasive lack of data on BONY life-stage-specific mesohabitat preferences in its rating of link understanding of the effects of mesohabitat conditions on other components of each life stage model:

- BONY fry and juveniles are thought to seek out or survive and grow better in backwaters or inundated flood plain wetlands as rearing habitat (Christopherson et al. 2004; Brunson and Christopherson 2005; Modde and Haines 2005; LCR MSCP 2016; Bestgen et al. 2017). Given the limited swimming ability of BONY fry, and consequently the dominance of drift in transporting the fry from their natal sites to suitable rearing habitat, the availability and spatial arrangement of interception habitat along the drift path likely also affected the ability of BONY fry to successfully encounter and move into rearing habitat.
- Adults in riverine settings, and juveniles following their departure from wild rearing habitats, appear to prefer swift runs and riffles, point bars, and pools and eddies adjacent to swift currents in main channels, at least when moving through these settings (Bestgen et al. 2006, 2008; Bozek et al. 1984; Joseph et al. 1977; Kaeding et al. 1986; LCR MSCP 2016; Minckley and Thorson 2007; USFWS 2002; Valdez and Clemmer 1982). These reported settings vary widely in total depth, and BONY move throughout the water column in these settings. Minckley (1991), for example, described BONY moving up and down in mid-channel between near-surface, mid-water, and bottom depths seeking food. As discussed above, BONY also move up in the water column at night and down during daylight. Perhaps, more significantly, as discussed above (see chapter 1, “BONY Reproductive Ecology”), accumulating evidence and anecdotal experience of LCR MSCP biologists (Lantow 2018) suggest that BONY adults prefer off-channel rather than active channel mesohabitats, even when not spawning.
- Adult, hatchery-reared BONY released into Lake Mohave, Lake Havasu, and the Bill Williams River National Wildlife Refuge appear to move preferentially into shallower waters, where they seek out stands of bulrush or cattail when present, particularly during daylight (Karam et al. 2011, 2012, 2013; Humphrey et al. 2014, 2016), and disperse less in more turbid environments (LCR MSCP 2016). Reports of juveniles and adults in impoundments in general, including isolated ponds, note that BONY concentrate during the day in settings that provide dense cover, such as submerged and emergent vegetation (Karam et al. 2011, 2012, 2013; Humphrey et al. 2014, 2016), or riprap with cavities into which the fish insert themselves apparently to avoid predators (Marsh and Mueller 1999; Mueller 2006; Marsh et al. 2013a), moving into open water to feed at

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night. Marsh et al. (2013a) also observed that, once released, adult BONY found a local setting within CHLP that provided suitable cover, such as a particular cavity in levee riprap, they tended to return to that same location every night.

- As discussed in chapter 1 (see “BONY Reproductive Ecology”), increasing evidence indicates that BONY prefer low-velocity and backwater mesohabitats for spawning. BONY do not appear to have strong preferences for substrate type in such settings. For example, BONY spawning has been observed in reservoirs over “gravel shelves” at depths up to 10 m (Bozek et al. 1984) and in isolated ponds over near-shore gravel shallows with as little as 0.5 m depth but adjacent to deeper water (Mueller 2006; LCR MSCP 2016, 2017). Gobalet and Wake (2000) and White and Roth (2009) report evidence of Native American use of stone weirs to trap spawning BONY along gravel shores of ancient Lake Cahuilla. In contrast, Bestgen et al. (2017) record BONY spawning in off-channel wetlands on predominantly silty substrates. Similarly, LCR MSCP biologists in 2018 observed BONY spawning mid-day at IPCA Pond 2 over silty substrate at a depth of approximately 2 m (Lantow 2018).

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

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

Mesohabitat structure similar to historic conditions presently occurs only in a few places where the channel is confined by bedrock and at tributary confluences. Otherwise, today, mesohabitat structure depends on main stem water storage-

delivery system design and operations, tributary inflows, channel and shoreline engineering, and the effects of macrohabitat structure. Dams have eliminated almost all inputs of sediment and large woody debris (Minckley and Rinne 1985) from the upper to the lower Colorado River and from one LCR reach to the next. Remnants of individual historic mesohabitat sites persist, and some may serve as spawning sites (Minckley et al. 1991; USFWS 2002; LCR MSCP 2016).

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. This element refers to the possibility of capture, examination, tagging, removal, and experimental treatment of BONY during scientific studies focused on the LCR, its backwaters, and its isolated ponds. This element does not refer to the scientific study of BONY at hatcheries or rearing facilities.

Monitoring of BONY along the LCR can involve their capture by a variety of methods, followed by examination, tagging, and, in most cases, return to the waterbody from which they were captured. Detection and capture methods and their associated sampling designs vary in their suitability for different mesohabitats, in their likelihood of encountering BONY of different sizes and life stages, and in their effects on captured individuals (Tyus et al. 1999; Mueller et al. 2004, 2005; Paukert et al. 2005; Mueller 2006, 2007; Ward 2006; Bestgen et al. 2008; Kesner et al 2008, 2010a, 2010b; Montony 2008; Pacey and Marsh 2008a; Ward et al. 2008; Portz 2009; Karam et al. 2011, 2012, 2013; Dowling et al. 2011; Hunt et al. 2012; Pearson et al. 2016). BONY adults appear to be particularly vulnerable to stress during capture and handling (Tyus et al. 1999; Paukert et al. 2005; Mueller 2006; Montony 2008; Pacey and Marsh 2008b; Portz 2009). For example, Mueller (2006) provides a detailed discussion of the frequent incidence of ruptured muscle syndrome among BONY adults captured by netting at CHLP, leading to death, which he equated with capture myopathy (Spraker 1993).

Genetic and demographic studies of BONY released to spawn in isolated ponds involves the capture and recording of BONY larvae and young of year (YOY) for genetic analysis (Osborne and Turner 2014, 2015, 2016, 2017). The genetic analysis is carried out on fin clips. No data are available on mortality among the captured larvae or YOY. It is not known whether BONY larvae or YOY experience stress-related mortality such as observed among adult BONY, described above. BONY behaviors, in turn, can affect monitoring efforts. In particular, BONY use of dense aquatic macrophyte stands as cover can interfere

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with efforts to track (i.e., to telemetrically contact) individuals released with electronic tag implants that move into such habitat (Karam et al. 2013; Humphrey et al. 2014, 2016; Best et al. 2017).

As noted in chapter 3 (see “Resting/Hiding”), BONY resting/hiding behavior in all motile life stages potentially may affect the likelihood of their detection and/or capture during monitoring. Specifically, the detection rates of different tracking methods (e.g., PIT tag monitoring) may differ when BONY are at lesser versus greater depth, in open water versus hiding in cover habitat, or in water with high versus low turbidity (see chapter 4, “Turbidity”). For example, investigators report that BONY use of dense aquatic macrophyte stands as cover can interfere with efforts to track (i.e., to telemetrically contact) electronically tagged individuals that move into such habitat (Karam et al. 2013; Humphrey et al. 2014, 2016; Best et al. 2017). The effectiveness of different methods for capturing BONY in open habitat (e.g., by electrofishing or various net-based methods) similarly may vary in relation to these same factors. These relationships between BONY behaviors and monitoring effectiveness are suggested more generally by studies of other native fishes in the Colorado River, including the closely related humpback chub (Bestgen et al. 2007; Rogers et al. 2008; Stone 2010; Van Haverbeke et al. 2013; Yackulic et al. 2018). Conversely, efforts to capture fishes may cause them to flee toward cover, resulting in a bi-directional relationship. For example, as noted in the original CEM report (Braun 2015), juvenile and adult BONY energetically try to leap out of floating pens and actively search for escape routes over, under, around, and through nets (Mueller 2006). Mueller (2006) also notes that BONY “...are easily captured from rearing ponds using recreational angling equipment. However, once a fish is hooked, it then becomes difficult to capture others, suggesting the fish may release fright pheromones.”

POST-REARING TRANSPORT AND RELEASE

This habitat element name has been shortened from the original, “Post-Rearing Transport and Release Methods,” and its definition has been updated as follows:

Full name: The transport and release hatchery-reared BONY, including the methods involved. This element refers to the collection, size selection, and transportation of BONY from hatcheries for release into the LCR main stem and reservoirs, backwaters, and isolated ponds; the types of locations and times of day and year during which they are released; whether they are tagged during this process for tracking following release; and whether or how they may be acclimated in situ to conditions at their release site. Some or all of these variables may affect BONY survival following release (e.g., by causing physiological stress or releasing them under conditions that reduce their ability to survive) (Bestgen et al. 2008, 2017; Karam and Marsh 2010; Karam et al. 2011,

2012, 2013; Kesner et al. 2008, 2010a, 2010b; LCR MSCP 2006; Marsh and Mueller 1999; Minckley and Thorson 2007; Montony 2008; Mueller 2006, 2007; Mueller et al. 2003a, 2004, 2005, 2014; Nesler et al. 2003; Pacey and Marsh 2008a, 2008b; Portz 2009; Sowka and Brunkow 1999; Sykes 2011, 2013; USFWS 2002.

Past and ongoing work tasks in the LCR MSCP annual work plans have sought or continue to address these possible cause-effect relationships, including: (1) past Work Task C39-Post-Stocking Distribution and Survival of Bonytail in Reach 3 and Work Task C46-Physiological Response in BONY and RASU to Transport Stress; and (2) current Work Task C61-Evaluation of Alternative Stocking Methods for Fish Augmentation, Work Task C63-Evaluation of Habitat Features that May Influence Success of Razorback Sucker and Bonytail in Backwater Environments, Work Task C64-Post-Stocking Movement, Distribution, and Habitat Use of Razorback Suckers and Bonytail, and Work Task C65-Evaluation of Immediate Post-Stocking Survival of Razorback Sucker and Bonytail (LCR MSCP 2017).

In particular, current LCR MSCP Work Task C61-Evaluation of Alternative Stocking Methods for Fish Augmentation addresses two topics: (1) adverse effects of stocking and (2) post-stocking distribution and survival (LCR MSCP 2017). Stocking variables of interest include the season and time of day of stocking, stocking cohort size, and stocking location (Humphrey et al. 2014, 2015, 2016; Karam et al. 2011, 2012, 2013; Marsh and Mueller 1999; McCall et al. 2017; Mueller et al. 2014).

RASU provide a possible analogy: The literature concerning RASU may indicate additional variables for consideration. Investigators have long reported that, immediately upon release, hatchery-reared RASU tend to scatter over long distances, particularly in the downstream direction (Foster and Mueller 1999; LCR MSCP 2006, 2015; Mueller and Burke 2005; Mueller and Foster 1999; Mueller and Marsh 1998; Mueller et al. 2003b; USFWS 2002; Valdez et al. 2012b). This is generally termed a “fright response” to the novelty of the environment into which the RASU are released. No studies have yet determined specifically what properties of the release environment trigger this response.

Investigators have proposed reducing this unwanted response among hatchery-reared RASU by releasing them initially into pens, rather than directly into open waters, to allow them to acclimate to the novel environment for a few days (e.g., Valdez et al. 2012b). Foster and Mueller (1999), Mueller and Foster (1999), and Mueller et al. (2003b) experimented with acclimating tagged RASU in holding pens in backwaters prior to release into Lake Powell and the Green River. These experiments compared the pen-acclimated RASU to other tagged RASU released at the same time without acclimation in holding pens. Both the pen-acclimated and non-acclimated RASU dispersed rapidly upon release into the open environment, but within 2 weeks the pen-acclimated RASU slowed,

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stopped, or reversed course, while the non-acclimated suckers continued to move downstream. After 4 weeks, the originally pen-acclimated RASU had cumulatively moved far less distance from the release site. After 2 months, the investigators concluded that acclimation in holding pens reduced both the range and rate of short-term dispersal; however, the experiments did not assess the effects of acclimation on survival.

The LCR MSCP has initiated its own such experiments with RASU, which it terms “soft release treatments” under Work Task 61 (LCR MSCP 2017). The LCR MSCP experimental treatment involves holding released, electronically tagged RASU for 3 days “...in a netted off section of a selected backwater compared to fishes released without being held. These soft releases should allow the fish recovery and acclimation time following the stresses of handling and hauling. This work will be accomplished using paired releases at three locations within Reach 3.” The released fish will be tracked over a longer period, “...in order to assess the effect on long-term survival (probability of re-contact).”

Hatchery-reared BONY also disperse quickly from their release sites when they are released into the river or impounded river reaches (Marsh and Mueller 1999; Karam et al. 2011, 2012, 2013; Humphrey et al. 2014, 2015, 2016; Mueller et al. 2014; LCR MSCP 2015; McCall et al. 2017). The ranges of dispersal distances appear roughly similar between BONY and RASU, although there does not appear to be a preference for downstream dispersal among BONY. Humphrey et al. (2014) also caution that, when large predatory fish such as striped bass (*Morone saxatilis*) consume BONY, and therefore ingest the PIT tags of the consumed fish, the subsequent movements of the PIT tag may be mistaken for movements of the original BONY. Experimentation with released BONY under LCR MSCP Work Task 61 has the potential to evaluate whether soft release methods could also benefit post-release survival for this species as well.

PRE-RELEASE CONDITIONING

The topic of pre-release conditioning of native fishes reared in hatcheries for release has received further attention in recent years. The definition of this habitat element therefore has been updated as follows:

Full name: The types and extent of pre-release conditioning of reared BONY physiology and behavior. This element refers to the pre-release conditioning of reared BONY to the range of environmental conditions they will encounter upon release, including flow velocities, water temperatures, habitat types, food items, infectious agents, and predator attention/attacks. Hatcheries generally try to condition their fishes to a relatively natural range of water temperatures, necessarily strive to minimize exposures to infectious agents, and necessarily rely on manufactured foods, but they have limited abilities to provide natural habitat

types. On the other hand, a growing literature proposes or indicates that conditioning for swimming performance and predator avoidance can increase survival among repatriated RASU and BONY (e.g., Avery et al. 2011; Bestgen et al. 2017; Garnett 2016; Kegerries and Albrecht 2009; LCR MSCP 2006, 2015; Lentsch et al. 1995; Mann et al. 2017; Mueller 2007; Mueller et al. 2007; O’Neill and Stewart 2014, 2015; O’Neill et al. 2013, 2016; Pacey and Marsh 2008a; Portz 2009; Schooley et al. 2008; Ward and Figiel 2013; Ward et al. 2007; Ward and Hilwig 2004; Wydoski and Wick 1998; Zelasko et al. 2009, 2010, 2011;) (see “Water Flow/Turbulence,” this chapter). Such conditioning is a topic of broad interest in fisheries restoration studies general (e.g., Archer and Crowl 2014; Oldenburg et al. 2011; Olson et al. 2012).

The LCR MSCP, prior to 2016, investigated the potential benefits of conditioning swimming abilities among reared BONY prior to release under Work Task C11-Bonytail Rearing Studies, and since then under Work Task C61-Evaluation of Alternative Stocking Methods for Fish Augmentation (LCR MSCP 2017). Trials are underway with various methods for conditioning BONY through exposure to aquatic predators or associated olfactory signals (Garnett 2016; LCR MSCP 2015, 2017; O’Neill et al. 2011, 2016; O’Neill and Stewart 2014, 2015).

The trials with BONY exposure to predators focus exclusively on conditioning BONY reactivity to aquatic predators. As discussed elsewhere in this CEM update, avian predation appears to be a significant cause of mortality among released BONY (see chapter 1, “BONY Reproductive Ecology”; chapter 3, “Predation” and “Swimming” and “Birds and Mammals,” this chapter). Anecdotal observations indicate that BONY have at least some natural reactivity to birds overhead and either avoid approaching the water surface during daylight or seek vegetative cover when in shallows – behaviors that would tend to reduce exposure to avian predators (Montony 2008; see also chapter 3, “Predation,” and “Aquatic Macrophytes”; and “Mesohabitat Structure,” this chapter). However, hatcheries typically strive to reduce the vulnerability of reared fishes in open ponds to avian predators (e.g., by covering the ponds with protective netting and/or dyeing their waters blue) (O’Neill et al. 2011; Ward et al. 2007). As a result, released BONY may lack a natural repertoire of responses to the potential for avian predation. For example, Mueller (2006) observed stocked BONY in relatively clear water at CHLP aggregating at the water surface during daylight hours. Such behavior could be a carryover from feeding behaviors learned in the hatchery. Conditioning hatchery-reared BONY to behave in ways that reduce their vulnerability to avian predation presumably would require different methods than those applied to condition their reactivity to aquatic predators.

Growing BONY to larger sizes before release may also be considered a form of pre-release conditioning. Bestgen et al. (2017) note, “The effects of [BONY] size at stocking into the upper Colorado River are the focus of ongoing analyses, as larger fish may survive at higher rates (Badame and Hudson 2003; Nesler et al.

2003; Zelasko et al. 2010).” However, as noted above (see chapter 3, “Predation”) the effects of BONY size on survival, among released BONY, is not currently a topic of investigation (LCR MSCP 2017).

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 BONY in each life stage and its pattern of variation over time and among macro- and mesohabitat settings. Historically, turbidity levels along the LCR and across its backwaters and their patterns of variation over time and space depended on main stem and tributary flows, channel and backwater geometry, and sediment loads. The Colorado River prior to its regulation was highly turbid, especially along its main channel and during flow pulses, with lower turbidity along channel margins and in off-channel settings (Ohmart et al. 1988; Minckley 1991; NRC 1991). BONY evolved in this environment, and turbidity therefore presumably affects—both directly and indirectly—several aspects of BONY ecology.

River regulation has drastically altered the turbidity regime of the main stem LCR, trapping most of the river’s natural sediment load in impoundments behind dams (NRC 1991). However, turbidity levels, the spatial extent and persistence of turbidity pulses, and their variation in the modern regulated river still depend on flow rates and turbulence, a habitat element affected by main stem water storage-delivery management, tributary inflows, and both macro- and mesohabitat structure. Specifically, elevated discharge from one of the dams or pulses of elevated discharge from tributaries such as the Bill Williams River (e.g., Humphrey et al. 2016) may deliver pulses of suspended sediment to the river or one of its impoundments, resulting in episodes of elevated turbidity along the affected river reach. Other factors affecting turbidity levels, the spatial extent and persistence of turbidity pulses, and their variation in the modern regulated river include channel and shoreline engineering (LCR MSCP 2004), nuisance species introduction and management, aquatic macrophyte distributions, and (in a feedback relationship) planktonic and benthic (periphyton) productivity.

Changes in the lake level, for example, can expose formerly submerged fine sediments, particularly in deltaic mesohabitats, where the exposed sediments are

subject to “erosion and suspension by river currents and wave action, resulting in increased turbidity levels at the inflow” (Valdez et al. 2012a). As noted elsewhere (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 (Kadlec and Knight 1996; Mitsch et al. 2005; Faber-Langendoen et al. 2008). Bioturbation of benthic sediments, such as by common carp during feeding and spawning (Rogers et al. 2008; Cucherousset and Olden 2011), or by mayfly larvae (Osterling et al. 2007), also may cause localized increases in turbidity for the duration of the disturbance. Nuisance species may also affect turbidity when algae form blooms or, conversely, when non-native quagga (*Dreissena bugensis*) and zebra mussels (*Dreissena polymorpha*) filter out large amounts of plankton and POM.

Turbidity directly affects several critical BONY behaviors such as navigating to and from sites for spawning, resting, and foraging; avoiding mechanical stress during flood pulses; and avoiding predators (Smith et al. 1979; Tyus and Minckley 1988; USFWS 2002; Modde and Haines 2005; Bestgen et al. 2006; Mueller 2006; Kesner et al. 2008; Pacey and Marsh 2008b; Karam et al. 2011, 2012, 2013; Marsh et al. 2013a; LCR MSCP 2016). Primary productivity (see “Invertebrates and Particulate Organic Matter,” this chapter) and competitor and predator behaviors vary with turbidity levels due to their effects on light penetration and sighting distances, and many non-native fishes avoid levels of turbidity that native fishes such as BONY readily tolerate (Paulson et al. 1980; Bestgen et al. 2006). The effects of turbidity on BONY survival and non-native fish behavior therefore are the subject of ongoing research interest (Mueller 2007; Valdez et al. 2011; Mueller et al. 2014; Humphrey et al. 2014, 2015, 2016; Vaage et al. 2015).

Vaage et al. (2015) (see also Ward et al. 2016) found that elevated turbidity protected Colorado River native fishes, including BONY, from depredation by most non-native fishes more than any other environmental factor. The factors examined included turbidity, vegetative cover such as aquatic macrophytes and flooded terrestrial vegetation, and rocky substrates with crevices. The study found significant reductions in predation on Colorado River native fishes, including BONY, 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. (2014, 2015, 2016) found that BONY released into Lake Havasu, including into the Bill Williams River confluence, generally tended to remain closer to their release sites, could be recontacted closer to the water surface, and survived longer when released into areas of higher turbidity. However, the results were not highly consistent, and other factors, such as the presence of other forms of cover (rocky crevices, overhangs, aquatic macrophytes), may also have affected BONY movement following release. Humphrey et al. (2016) also note that flathead catfish prefer

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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), and the effects among BONY observed anecdotally by Vaage et al. (2015) and Humphrey et al. (2014, 2015, 2016) are consistent with this general expectation.

Turbidity also may affect monitoring, capture, and handling of RASU for scientific study, as discussed above (see chapter 3, “Monitoring, Capture, 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 fish by monitoring methods that require visual contact, including recovery of individuals stunned by electroshocking and (2) they attenuate transponder signals (recently Bestgen et al. 2007; Rogers et al. 2008; Stone 2010; Van Haverbeke et al. 2013).

WATER CHEMISTRY

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 BONY. This element refers to the water chemistry at sites potentially used by BONY in each life stage, including the way that water chemistry may vary over time and space. The element covers parameters such as DO, pH, salinity, naturally occurring dissolved substances, and contaminants such as added nitrate/nitrite, perchlorate, selenium, several metals, and artificial organic compounds (Bureau of Reclamation [Reclamation]; Hinck et al. 2007, 2009; LCR MSCP 2004; 2010, 2011a, 2011b, 2017; Ohmart et al. 1988; Patiño et al. 2012; Seiler et al. 2003; Stolberg 2009, 2012; Turner et al. 2011). Contaminants in the LCR arrive from both point and non-point sources (see “Updates to Chapter 5 – Controlling Factors”). Water storage-delivery system design and operations (see chapter 5) also affect water chemistry, including salinity and DO concentrations, through their effects on reservoir operations and releases, diversions and flow management for off-channel wetlands and ponds, and well-water supplies to ponds (see below). Numerous habitat elements affect water chemistry at any given location, particularly water depth, temperature, circulation, and their variation over time.

As discussed in chapter 3 (see “Chemical Stress”), BONY during different life stages are known or suspected to be vulnerable to stress from changes in water chemistry, either from direct exposure to harmful conditions in the water column or from the consumption of contaminants that have bioaccumulated in invertebrates on which BONY feed (Bulkley et al. 1982; Pimentel and Bulkley 1983; Buhl and Hamilton 1996; Buhl 1997; Canton 1999; USFWS 2002;

Hamilton 2003; Tomasso et al. 2003; Dwyer et al. 2005; Mueller 2007; Paretto 2007; Pacey and Marsh 2008b; Walker et al. 2009; Gwinn 2011; May and Walther 2013; LCR MSCP 2017).

As noted in chapter 1 (see “BONY Reproductive Ecology”), when given the opportunity to move among habitats, BONY tend to select water with high levels of total dissolved solids and can persist in water with total dissolved solid concentration up to 4,700 mg/L (Pimentel and Bulkley 1983). This is “the highest tolerance [for salinity] reported for any species of Colorado River” in the genus *Gila* (LCR MSCP 2016). Similarly, the LCR MSCP (2017; see also Stolberg 2009, 2012) has found that BONY eggs and larvae have higher tolerances (exhibit lower rates of mortality) at elevated salinity (measured as specific conductance) than do RASU eggs and larvae.

Alterations to water chemistry along the LCR, specifically nutrient enrichment, also affect planktonic and benthic primary productivity (Ohmart et al. 1988; NRC 1991; Melis et al. 2010), which in turn affect turbidity. However, productivity along the LCR may be more limited by the availability of phosphorus than that of nitrogen (Turner et al. 2011). As noted above (see “Invertebrates and Particulate Organic Matter,” this chapter), the LCR MSCP has experimented with fertilizing off-channel habitats around the margins of Lake Mohave using both dissolved nutrients and POM. These experiments were conducted in order to determine if such mechanical fertilization stimulates primary and/or secondary productivity (Loomis 2014). The results have been ambiguous, affected by high variability among test sites and within individual test sites over time, and impacts of poor water circulation, DO depletion during hot weather, and algal mat formation. As also noted above concerning invertebrates along the LCR (see “Invertebrates and Particulate Organic Matter,” this chapter), toxins released by golden alga (*Dreissena polymorpha*) blooms could also harm BONY in backwaters and other waterbodies with limited water circulation.

Pheromones and other olfactory cues in the water presumably provide BONY with much needed information about their environment. BONY release “alarm” or “fright” pheromones when they detect threats such as predators, and this mechanism potentially can be used to help condition BONY to avoid predators (Mueller 2006; Mueller et al. 2007; LCR MSCP 2015; O’Neill and Stewart 2014, 2015; O’Neill et al. 2013, 2016). Gwinn (2011) also notes that contaminants can affect the olfactory process in fishes and therefore affect their fright reactions. Releases of pheromones presumably could be involved in triggering BONY spawning, although data are lacking.

WATER DEPTH

No change.

WATER FLOW, TURBULENCE

As discussed in chapter 1 (see “BONY Reproductive Ecology”), new information since completion of the original BONY conceptual ecological model (Braun 2015) reinforces the understanding that BONY spawning may be triggered more by general seasonal patterns in temperature and photoperiod than by any specific thermal event(s). The literature continues to indicate also that flow conditions play little role in triggering spawning. On the other hand, as discussed above (see chapter 1, “BONY Reproductive Ecology,” and “Mesohabitat Structure,” this chapter), BONY increasingly appear to prefer to spend most of their time in low-velocity environments and appear to select spawning sites in part based on flow velocity. As noted in chapter 1 (see “BONY Reproductive Ecology”), Osborne and Turner (2017) specifically note from their studies of the Lake Mohave backwater ponds, 2014–16, and IPCA Pond 2, 2017, “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 among both males and females may be higher in the backwaters than in lotic systems.”

WATER TEMPERATURE

As discussed in chapter 1 (see “BONY Reproductive Ecology”), new information since completion of the original BONY conceptual ecological model (Braun 2015) reinforces the understanding that BONY spawning may be triggered more by general seasonal patterns in temperature and photoperiod than by any specific thermal event(s). As discussed in chapter 3 (see “Swimming”), new findings also reinforce the existing understanding of the effects of water temperature on BONY swimming performance.

Updates to Chapter 5 – Controlling Factors

BONY MONITORING AND CONSERVATION PROGRAMS

This controlling factor replaces the original “Augmentation Program Operations” so that the CEM better captures the key drivers of habitat manipulation, the new habitat element, “Genetic Diversity”; the updated habitat element, “Monitoring, Capture, Handling” (formerly “Scientific Study”); and the new critical biological process, “Hybridization.” The updated definition for this controlling factor is as follows:

The U.S. Department of the Interior classified BONY as an endangered species (per the U.S. Endangered Species Act of 1973) in 1980, identified the LCR ecosystem as part of the critical habitat for the species, approved a recovery plan for the species in 1994, and approved recovery goals in 2002 (USFWS 2002). The LCR MSCP assumed lead responsibility for BONY conservation efforts in the LCR ecosystem in 2005. The recovery effort includes maintaining a broodstock of BONY in hatcheries due to the disappearance of all wild populations, with controls to maintain genetic diversity; releases of hatchery-reared BONY to riverine, main-stem impoundments, and off-channel habitat; and monitoring and research to support adaptive management.

The controlling factor, “BONY Monitoring and Conservation Programs,” addresses the activities of Reclamation, the USFWS, and the States and Tribes in managing the joint BONY augmentation program (LCR MSCP 2006, 2015). The augmentation program covers all efforts, including maintaining the health, genetic diversity, and fertility of the BONY broodstock; conditioning cohorts to ranges of flow and temperature conditions and predator interactions they will likely encounter after release; and assembling, transporting, and releasing size-appropriate cohorts into LCR Reaches 3–5, including into ponds in created backwater habitat.

The present controlling factor also addresses the monitoring, research, and conservation actions of Reclamation, the USFWS, the States and Tribes, and partners in support of the recovery effort. 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 2017) that describes, in detail, the activities of the program.

CHANNEL AND OFF-CHANNEL ENGINEERING

This controlling factor replaces the original “Channel, Lake, and Pond Design and Operations,” primarily to standardize naming, with a slightly updated definition as follows:

This factor addresses the activities of Reclamation, the USFWS, and the States and Tribes in managing the geomorphology of the river channel and off-channel habitats, including depth profiles, shorelines, and substrates. It covers historic and ongoing activities such as dredging, shoreline armoring, construction and maintenance of river levees and training structures, construction and maintenance of connected backwater environments, and other modifications in areas of intense development or intensive habitat management (LCR MSCP 2004, 2017). These activities strongly shape the macrohabitat structure, mesohabitat structure, and sediment dynamics, and moderately shape depth profiles throughout the system; however, there are few areas of active mechanical shaping along channel and off-channel habitats, and only infrequent (less often than annual) maintenance or alteration (LCR MSCP 2017). Channel, shoreline, and backwater management activities, such as dredging and bank and training structure maintenance, can disturb sediment in ways that also may produce localized turbidity that disperses with distance from the activity. The LCR MSCP Habitat Conservation Plan specifically recognizes this as one of the ways in which Federal actions may routinely affect BONY (LCR MSCP 2004); however, the effects will be localized and brief due to the limited flow velocities present in the regulated LCR.

MOTORBOAT ACTIVITY

No change.

NON-BONY FISHERIES

This controlling factor replaces the original “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 BONY, 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 (<https://www.azgfd.com/fishing/species/>) and State records for any caught along the LCR (<https://www.azgfd.com/Fishing/records/>).

Management of sport fisheries includes regulating fishing activities and introducing and/or stocking sport species as well as bait and forage species for the sport fisheries. These management activities and the legacies of past such activities may affect the LCR ecosystem in several ways, including introducing infectious agents, shaping public perceptions of the relative value of sport fisheries versus native species recovery programs, shaping the spectrum of species that prey on or compete with BONY, and altering physical habitat. The potential for conflicts between sport fishery management and the conservation of native fishes along the Colorado River in fact is a longstanding concern (Holden 1991; Minckley 1991; NRC 1991; Rolston, III 1991; Mueller and Marsh 2002; Minckley et al. 2003; Marsh and Pacey 2005; Clarkson et al. 2005). Table 3, (chapter 4) lists non-native sport species introduced into the LCR ecosystem and species introduced as bait or forage species for the sport fisheries. Table 3 also indicates whether each species is known to prey on or compete with RASU or could be proposed as predators or competitors based on their feeding ecology. Infectious (including parasitic) organisms that are known to infect BONY and likely introduced with non-native sport fishes include *Lerneae* spp. and *Myxobolus* spp. (Flagg 1982) (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 BONY. Three of these are covered under the Habitat Conservation Plan (LCR MSCP 2004)—flannelmouth suckers (*Catostomus latipinnis*), humpback chubs, and RASU—and one, the 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 BONY.

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

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The LCR MSCP (2017) also suspects illegal introductions as the source of the largemouth bass found in ponds being used in conditioning experiments in late 2016.

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 “Water Storage/Delivery System Design and Operations” simply to standardize naming.

Updates to Chapter 6 – Conceptual Ecological Model by Life Stage

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. The items listed below do not include changes that involve only updates to names. These latter changes do not require further documentation here (see “Summary of Standardization of Terms,” this chapter).

NEW LINKS WITH CONTROLLING FACTORS AS CAUSAL AGENTS

- BONY Monitoring and Conservation Programs (CF) effects on Aquatic Macrophytes (HE): Aquatic/emergent vegetation management at off-channel ponds can affect availability of this vegetation as cover habitat for BONY, as was the case at the IPCA where dense stands of macrophytes were removed during pond restoration ca. 2015–16. The LCR MSCP presumably also could try to manipulate shoreline vegetation around the margins of Lakes Mohave and Havasu, although not within the USFWS wildlife refuges. Link intensity has the potential to be high but, in practice, will vary (average = medium intensity), but with low spatial and temporal scale ratings. 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.*
- BONY Monitoring and Conservation Programs (CF) effects on Channel and Off-Channel Engineering (CF): The LCR MSCP and its partners can and do modify channel and off-channel physical habitat in the interests of meeting the program’s goals or conducting experiments (e.g., pond fertilization; other projects done with ponds disconnected from the channel). Such changes have varying intensity (average = medium intensity) but low spatial and temporal scales. The pulses are spatially predictable but temporally less so, and intensity can vary unpredictably. The processes involved are well understood. *Applies to all life stages.*
- BONY Monitoring and Conservation Programs (CF) effects on Genetic Diversity (HE): The rearing program is designed and carefully monitored to avoid further reductions in BONY genetic diversity stemming from the small number of individuals from which the current broodstock originates. There is no recruitment taking place among released BONY that could

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further affect genetic diversity; therefore, link intensity and spatial and temporal scale ratings are all high. In the absence of in situ recruitment, predictability and understanding are both high as well. *Applies to all life stages.*

- BONY Monitoring and Conservation Programs (CF) effects on Hybridization (CAP): The locations at which the hatchery program releases BONY could affect the potential for hybridization, if those locations are within the current distributions of other *Gila* species, particularly the humpback chub, with which BONY have previously hybridized. *This only affects the Spawning Adults life stage.* Link intensity, spatial scale, and temporal scale ratings are all low because, at present, the LCR MSCP releases BONY into very few locations in the LCR ecosystem where any other *Gila* species may occur: roundtail chub occur in the Bill Williams River but presently only upstream of Alamo Lake (Shafroth and Beauchamp 2006; Buechel et al. 2016). Predictability and understanding are high because the LCR MSCP has high control of this relationship and the distributions of other *Gila* species in the LCR ecosystem are well known.
- BONY Monitoring and Conservation Programs (CF) effects on Monitoring, Capture, Handling (HE): *This is a new link for Eggs and Early Larvae*, but it is an existing link for all other life stages. All fields for Eggs and Early Larvae are the same as for the other life stages except as follows: (1) The “Link Reason” field states simply, “The BONY Monitoring and Conservation Program includes a significant component of scientific study of released BONY and their offspring (if any are found). However, these studies to date address only BONY fry and older life stages in the LCR, its backwaters, and its isolated ponds, and do not appear to address eggs or early larvae.” All other “reason” fields state only “See Link Reason.” (2) Link intensity, spatial scale, and temporal scale ratings are all low. The rating for predictability is medium and the rating for understanding high because the relationship of the BONY Monitoring and Conservation Program to the scientific study of BONY fry or juveniles is well understood.

UPDATED LINKS WITH CONTROLLING FACTORS AS CAUSAL AGENTS

- BONY Monitoring and Conservation Programs (CF) effects on Monitoring, Capture, Handling (HE): Link intensity is updated to high. The link spatial and temporal scale ratings are set at low because few BONY are recontacted in the field after release or, in protected ponds, are

contacted often as they grow. *Applies to all life stages except Eggs and Early Larvae*, for which this is a new link entirely. The latter life stage, at present, is not subject to monitoring, capture, or handling in the field, so its link intensity, spatial scale, and temporal scale ratings are all low.

- BONY Monitoring and Conservation Programs (CF) effects on Post-Rearing Transport and Release (HE): Link intensity is updated (downgraded) to medium: more acclimation using holding pens at release sites should be explored to improve orientation and acclimation, and reduce fright response. *Applies to Newly Stocked Adults only.*
- BONY Monitoring and Conservation Programs (CF) effects on Pre-Release Conditioning (HE): Link intensity is updated to low. This CF is the only factor determining whether more conditioning of swimming capabilities and predator avoidance might be implemented. The rating of intensity, as with the ratings of spatial and temporal scales, is low because the work is only experimental and limited in scope at present. *Applies to Newly Stocked Adults only.*
- Tributary Inflows (CF) effects on Turbidity (HE): Link intensity is updated to high. Inflows from major tributaries such as the Bill Williams River create distinct zones of turbidity following runoff events, although, as indicated in the ratings for spatial and temporal scales, the turbidity may be present only briefly and within a relatively small area relative to the size of the system overall. *Applies to all life stages.*

NEW LINKS WITH HABITAT ELEMENTS AS CAUSAL AGENTS

- Genetic Diversity (HE) effects on Chemical Stress (CAP): This link identifies one possible way in which reduced genetic diversity could affect BONY following release – in this case, by limiting their ability to respond to potentially chemically stressful conditions such as exposure to anthropogenic contaminants or exposure to extremely low concentrations of DO or elevated salinities. 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, with no known threshold, and unidirectional. Link intensity is unknown, but both spatial and temporal scales are estimated to be high: Theoretically, this relationship could be important, but the literature does not indicate whether and how it actually matters for

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BONY. The spatial and temporal scale ratings are potentials. Under present circumstances, BONY experience 100% mortality following release, except in isolated ponds, so any effects are not experienced by any “wild” population. Link predictability and understanding correspondingly are low. *Applies to all life stages.*

- Genetic Diversity (HE) effects on Disease (CAP): This link identifies one possible way in which reduced genetic diversity could affect BONY following release – in this case, by limiting their ability to respond to new and old 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, with no known threshold, and unidirectional. However, while the fact that genetic diversity can affect susceptibility to disease is well established, the ways in which this occurs are complex. Link intensity is unknown, but both spatial and temporal scales are estimated to be high: Theoretically, this relationship is important, but the literature does not indicate whether or how it actually matters for BONY health and survivorship. The spatial and temporal scale ratings are potentials. Under present circumstances, BONY experience 100% mortality following release, except in isolated ponds, so any effects are not experienced by any “wild” population. Link predictability is low: The incidence of disease in any BONY that survive long enough following release in the LCR probably depends on many factors, of which genetic diversity is but one. Link understanding also is low: Theoretically, this relationship is important, but the literature does not indicate whether and how it actually matters for BONY health and survivorship. *Applies to all life stages.*
- Genetic Diversity (HE) effects on Swimming (CAP): This link identifies a possible way in which simply **altered** genetic diversity could affect BONY – in this case, by affecting the swimming morphology and/or performance characteristics of hybrid BONY. Berry and Pimentel (1985), Carveth et al. (2006), Moran et al. (2016), and Chandos (2017) all present evidence that swimming morphology and/or performance characteristics vary among bonytail, humpback chub, and roundtail chub, and that temperature affects performance slightly differently among the three species. These species were at least partially sympatric (likely over thousands to millions of years) in the Colorado River prior to regulation, with differences only in mesohabitat preferences (Kaeding et al. 1990; Minckley and Thorson 2007), and apparently sometimes crossed (Gerber et al. 2001; Minckley and Thorson 2007), yet maintained distinctiveness as species. No one has definitively shown how these species evolved and came to maintain their ecological differences. However, their differences in swimming performance, morphology (especially as related to

swimming), and mesohabitat preferences might suggest that natural selection weeded out individuals with intermediate characteristics; if that's the case, then hybridization in the absence of those selective pressures (or in the presence of different selective pressures) could result in differences in survival among hybrids. Link character is unknown, but the link is assumed to be unidirectional. Link intensity, spatial scale, and temporal scale are all unknown. Theoretically, this relationship could be important, but as indicated for the links from “BONY Monitoring and Conservation Programs” to “Hybridization” and from “Hybridization” to “Genetic Diversity,” the chances of hybridization of BONY with any other *Gila* species in the LCR ecosystem presently is low. Further, the possible effects of such hybridization-altered genetic diversity on BONY swimming abilities are unknown. Link predictability and understanding correspondingly are 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 reduced genetic diversity could affect BONY following release – in this case, by limiting their ability to respond to potentially thermally stressful conditions. Note, too, as discussed below concerning possible effects of genetic diversity on swimming, that hybridization potentially could affect swimming performance in ways related to water temperature (i.e., hybrids might exhibit differences from BONY statistical ranges in the ways in which water temperature affects swimming performance). Otherwise, in general, 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 temperature. The hypothesized relationship is proposed to be negative, with no known threshold, and unidirectional. Link intensity is unknown, but link spatial and temporal scales are proposed to be high: Theoretically, this relationship could be important, although the literature does not indicate whether and how it actually matters for BONY. Consequently, the spatial and temporal scale ratings are potentials. Under present circumstances, BONY experience 100% mortality following release, except in isolated ponds, so any effects are not experienced by any “wild” population. Link predictability and understanding correspondingly are low. *Applies to all life stages.*
- Post-Rearing Transport and Release (HE) effects on Swimming (CAP): This link refers to the possible use of holding pens at release sites in order to improve BONY orientation and acclimation to the environment into which they are being released and to reduce their fright response that results in their swimming away (dispersing from) the release site rather than taking advantage of any habitat protections it may offer. The hypothesized link accordingly is proposed to be complex and

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unidirectional. Link intensity is unknown, the link spatial scale is estimated to be low, and the link temporal scale is high: Theoretically, this relationship could be important, but no experiments have yet assessed it, so the intensity of effect is unknown. The spatial scale would be limited to release sites but would apply to all times when holding pens were used. Link predictability and link understanding correspondingly are both low. *Applies to Newly Stocked Adults only.*

- 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. Predatory birds and mammals may pay less attention to turbid locations because, assuming most are sight hunters, they will pay greater attention to locations where they are more able to see potential prey in the water. Beavers and muskrats, in turn, may prefer waters with lower turbidity for navigating or simply because the vegetation they prefer occurs more plentifully in settings with lower turbidity. The hypothesized link is proposed to have negative character, with no known threshold, and to be unidirectional. Link intensity is unknown, but the link spatial scale is estimated to be low and the temporal scale high: The link reason statement indicates why this relationship could have significant impact. However, 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, which also limits 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. Correspondingly, link predictability is unknown and link understanding 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, in which, as stated by Osborne and Turner (2017), “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 among both males and females [at Lake Mohave backwater ponds in 2014–16 and at IPCA Pond 2 in 2017] 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 and temporal scales are estimated to be 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 BONY attempt to spawn after release and all times when spawning occurs. Correspondingly, link predictability is unknown and link understanding low. *Applies to Spawning Adults only.*

UPDATED LINKS WITH HABITAT ELEMENTS AS CAUSAL AGENTS

- Aquatic Macrophytes (HE) effects on Resting/Hiding (CAP). Link understanding is updated to medium given the increasing evidence that BONY avoid predators effectively if aquatic macrophytes such as *Typha* and/or *Schoenoplectus* are available as cover. Limited spatial availability of such cover remains the main constraint on overall magnitude of effect, as indicated in the original CEM. *Applies to all life stages except Eggs/Early Larvae and Spawning Adults.*
- Birds and Mammals (HE) effects on Predation (CAP): Link intensity is updated to high based on new evidence of how severe this link can be, in the absence of protective turbidity or vegetative cover for BONY (Imperial Ponds experiments), given BONY propensity to use shallow mesohabitats where historically they would have been protected by turbidity. Link understanding is updated to medium based on accumulating evidence. *Applies to all life stages except Eggs and Early Larvae, for which there is no evidence of avian predation.*
- Monitoring, Capture, Handling (HE) Effect on Mechanical Stress: The link reason text is updated with information from the updated habitat element definition (see “Updates to Chapter 4 – Habitat Elements”). The link ratings remain unchanged. *Applies to all life stages except Eggs and Early Larvae because the updated definition only concerns later life stages.*
- Post-Rearing Transport and Release (HE) Effects on Chemical Stress (CAP): This link refers to the possible use of holding pens at release sites in order to improve BONY orientation and acclimation to the environment into which they are being released and to reduce their fright response that results in their swimming away (dispersing from) the release site rather than taking advantage of any habitat protections it may offer. *Applies to Newly Stocked Adults only.* The link reason is updated as follows, with all other fields left unchanged: Hatchery-reared BONY may experience stress as a result of variation in water properties such as DO levels during transport to and release into riverine, reservoir, protected backwater, or created habitat. Releasing the BONY into holding pens for 2–3 days could improve BONY orientation and acclimation to the larger environment into which they are being released and reduce their fright response that results in their swimming away (dispersing from) the release site rather than taking advantage of any habitat protections it may offer.

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- Post-Rearing Transport and Release (HE) effects on Mechanical Stress (CAP): This link refers to the possible use of holding pens at release sites in order to improve BONY orientation and acclimation to the environment into which they are being released and to reduce their fright response that results in their swimming away (dispersing from) the release site rather than taking advantage of any habitat protections it may offer. *Applies to Newly Stocked Adults only.* The link reason is updated as follows, with all other fields left unchanged: Hatchery-reared BONY may experience stress as a result of variation in water properties such as DO levels during transport to and release into riverine, reservoir, protected backwater, or created habitat. Releasing the BONY into holding pens for 2–3 days could improve BONY orientation and acclimation to the larger environment into which they are being released and reduce their fright response that results in their swimming away (dispersing from) the release site rather than taking advantage of any habitat protections it may offer.
- Post-Rearing Transport and Release (HE) effects on Thermal Stress (CAP): This link refers to the possible use of holding pens at release sites in order to improve BONY orientation and acclimation to the environment into which they are being released and reduce their fright response that results in their swimming away (dispersing from) the release site rather than taking advantage of any habitat protections it may offer. *Applies to Newly Stocked Adults only.* The link reason is updated as follows, with all other fields left unchanged: Hatchery-reared BONY may experience stress as a result of variation in water properties such as DO levels during transport to and release into riverine, reservoir, protected backwater, or created habitat. Releasing the BONY into holding pens for 2–3 days could improve BONY orientation and acclimation to the larger environment into which they are being released and reduce their fright response that results in their swimming away (dispersing from) the release site rather than taking advantage of any habitat protections it may offer.
- Turbidity (HE) effects on Aquatic Macrophytes (HE): Link character direction is updated to bi-directional. The 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 is updated to high, and the link predictability is updated to medium, based on increasing evidence that BONY avoid potential avian predators and most potential aquatic predators more effectively in turbid water. The limited spatial and temporal availability of sufficient turbidity in habitat zones of interest to BONY remains the main constraint on overall magnitude of effect. The

link reason is updated accordingly. Link understanding rating remains low. *Applies to all life stages.* The link magnitude reason statement is also updated as follows, with a similar modification to the link predictability reason: Vaage et al. (2015; see also Ward et al. 2016) found that elevated turbidity protected Colorado River native fishes, including BONY, 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. Humphrey et al. (2014, 2015, 2016) found that BONY released into Lake Havasu, including into the Bill Williams River confluence, survived longer when released into areas of higher turbidity. However, the results were not highly consistent and other factors, such as the presence of other forms of cover (rocky crevices, overhangs, and aquatic macrophytes) may also have affected BONY movement following release. However, depredation by flathead catfish, 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), and the effects among BONY observed anecdotally by Vaage et al. (2015) and Humphrey et al. (2014, 2015, 2016) are consistent with this general expectation. 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 BONY behaviors for predator avoidance in the face of turbidity. In settings where extended pulses of turbidity still occur, the intensity of this relationship would likely be greater.

- Turbidity (HE) effects on Resting/Hiding (CAP): Link intensity is updated to high, based on increasing evidence that BONY actively seek or remain in turbid water when apparently trying to hide from threats, including not only from predators but also from field investigators. The limited spatial and temporal availability of sufficient turbidity in habitat zones of interest to BONY remains the main constraint on the overall magnitude of effect. The link reason and link magnitude reasoning are updated accordingly, and link understanding is updated to medium. *Applies to all life stages except Eggs and Early Larvae and Spawning Adults. Resting/Hiding is not a valid critical biological activity or process for these latter two life stages.* The “Link Magnitude Reason” statement is also updated as follows: BONY 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. Humphrey et al. (2014, 2015, 2016) found that BONY released into Lake Havasu, including into the Bill

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Williams River confluence, survived longer when released into areas of higher turbidity. However, the results were not highly consistent and other factors, such as the presence of other forms of cover (rocky crevices, overhangs, or aquatic macrophytes) may also have affected BONY movement following release. 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 BONY behaviors for predator avoidance in the face of 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 is 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. The link reason and link magnitude reasoning are updated accordingly. All other fields remain unchanged. *Applies to all life stages.*
- Water Flow, Turbulence (HE) effects on Aquatic Macrophytes (HE): Link character direction is updated to bi-directional since aquatic macrophytes dampen wave action, flow velocities, and turbulence in those settings. The link reason and link magnitude reasoning are updated accordingly. Link intensity is updated to high. All other fields remain unchanged. *Applies to all life stages.*
- Water Temperature (HE) effects on Swimming (CAP) for all life stages except Eggs and Early Larvae: The link reason and link magnitude reason are updated, and link intensity is updated to high to recognize the effects of water temperature on swimming strength. *These changes apply to all life stages except Eggs and Early Larvae.*
- Water Temperature (HE) effects on Swimming (CAP) for Spawning Adults: Additionally, for Spawning Adults only, the link reason and link magnitude reason text are updated, and the link spatial and temporal scale ratings are updated to high to recognize that water temperature or temperature variation may be a cue that triggers spawning-related swimming behaviors. *Applies only to Spawning Adults.*

NEW LINKS WITH CRITICAL ACTIVITIES/PROCESSES AS CAUSAL AGENTS

- Chemical Stress (CAP) effects on new "... Growth" life-stage outcome for Eggs and Early Larvae, Fry and Juveniles, Newly Stocked Adults, and

Established Adults life stages: These links recognize that chronic chemical stress can inhibit BONY growth. 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 estimated to be high, but the link spatial and temporal scale ratings are low: Chronic chemical stress is a commonly recognized cause of impaired body condition and growth in fishes. However, BONY in the river, impoundments, and isolated ponds of the LCR ecosystem face few or no situations in which they experience chronic chemical stress. Correspondingly, link predictability and understanding are both high. *Applies to all life stages except Spawning Adults.*

- Disease (CAP) effects on new “... Growth” life-stage outcome for Eggs and Early Larvae, Fry and Juveniles, Newly Stocked Adults, and Established Adults life stages: These links recognize that chronic illness can inhibit BONY 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 illness can reduce growth and impaired condition can increase susceptibility to illness. Link intensity is estimated to be high, but the link spatial and temporal scale ratings are low: Chronic illness is a commonly recognized cause of impaired body condition and growth in fishes. However, BONY in the river, impoundments, and isolated ponds of the LCR ecosystem are so scarce that they experience few instances of disease before becoming food for some predator. Correspondingly, link predictability and understanding are both high. *Applies to all life stages except Spawning Adults.*
- Foraging (CAP) effects on new “... Growth” life-stage outcome for Fry and Juveniles, Newly Stocked Adults, and Established Adults life stages: These links recognize that foraging success affects BONY growth. Foraging success is a commonly recognized cause of healthy body condition in fishes. The hypothesized link is proposed to be positive, with no known threshold, and bi-directional: Foraging success promotes growth and healthy body condition, and impaired body condition can reduce foraging success. Link intensity is estimated to be high, but the link spatial and temporal scale ratings are low: Foraging success is a commonly recognized cause of healthy body condition in fishes. However, BONY in the river, impoundments, and isolated ponds of the LCR ecosystem appear to survive for only a few weeks at most before becoming food for some predator, and mostly do not disperse significantly from release sites, limiting the spatial extent and timespan across which this relationship can play out. Correspondingly, link predictability and understanding are both high. *Applies to all life stages except Eggs and Early Larvae and Spawning Adults.*

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- Hybridization (CAP) affects Genetic Diversity (HE) for all five life stages: These links recognize that BONY hybridization with other *Gila* species could affect genetic diversity in every life stage produced by in situ recruitment. However, no such in situ recruitment is taking place, so this relationship is purely hypothetical. The hypothesized link is proposed to be complex and unidirectional. Link intensity is unknown, but the link spatial and temporal scale ratings are both estimated to be low, for the multiple reasons discussed in chapter 3, “Hybridization.” Link predictability is unknown, and link understanding is low because the circumstances in which *Gila* hybridization predictably affects genetic diversity in the wild are not well studied or understood. *Applies to all life stages.*
- Mechanical Stress (CAP) effects on new “... Growth” life-stage outcome for Eggs and Early Larvae, Fry and Juveniles, Newly Stocked Adults, and Established Adults life stages: These links recognize that chronic mechanical stress can inhibit BONY 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 stress can reduce growth, and impaired condition can increase susceptibility to stress. Link intensity is high, but the link spatial and temporal scale ratings are low: Chronic mechanical stress is a commonly recognized cause of impaired body condition and growth in fishes. However, BONY in the river, impoundments, and isolated ponds of the LCR ecosystem face few or no situations in which they experience chronic mechanical stress. Correspondingly, link predictability and understanding are both high. *Applies to all life stages except Spawning Adults.*
- Resting/Hiding (CAP) effects on Monitoring, Capture, Handling (HE) in all motile life stages: BONY resting/hiding behavior in all motile life stages potentially may affect the likelihood of their detection and/or capture during monitoring. Specifically, the detection rates of different tracking methods (e.g., PIT tag monitoring) may differ when BONY are at lesser versus greater depth, in open water versus hiding in cover habitat, or in water with high versus low turbidity (see “Turbidity,” this chapter). For example, investigators report that BONY use of dense, aquatic macrophyte stands as cover can interfere with efforts to track (i.e., to telemetrically contact) electronically tagged individuals that move into such habitat (Karam et al. 2013; Humphrey et al. 2014, 2016; Best et al. 2017). The effectiveness of different methods for capturing BONY in open habitat (e.g., by electrofishing or various net-based methods) similarly may vary in relation to these same factors. These relationships between BONY behaviors and monitoring effectiveness are suggested more generally by studies of other native fishes in the Colorado River,

including the closely related humpback chub (Bestgen et al. 2007; Rogers et al. 2008; Stone 2010; Van Haverbeke et al. 2013; Yackulic et al. 2018). Conversely, efforts to capture fishes may cause them to flee toward cover, resulting in a bi-directional relationship. For example, as noted in the original CEM report (Braun 2015), juvenile and adult BONY energetically try to leap out of floating pens and actively search for escape routes over, under, around, and through nets (Mueller 2006). Mueller (2006) also notes that BONY "...are easily captured from rearing ponds using recreational angling equipment. However, once a fish is hooked, it then becomes difficult to capture others, suggesting the fish may release fright pheromones." 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 BONY. However, link spatial and temporal scale ratings are hypothesized to be high because the relationship should apply wherever and whenever BONY monitoring takes place. *Applies to all life stages except Eggs and Early Larvae.*

- Swimming (CAP) effects on Monitoring, Capture, Handling (HE) in all motile life stages: BONY swimming behavior in all motile life stages potentially may affect the likelihood of their detection and/or capture during monitoring. Specifically, the detection rates of different tracking methods (e.g., PIT tag monitoring) may differ when BONY are swimming at lesser versus greater depth, in open water versus hiding in cover habitat, or in water with high versus low turbidity (see "Turbidity," this chapter). For example, investigators report that BONY use of dense aquatic macrophyte stands as cover can interfere with efforts to track (i.e., to telemetrically contact) electronically tagged individuals that move into such habitat (Karam et al. 2013; Humphrey et al. 2014, 2016; Best et al. 2017). The effectiveness of different methods for capturing BONY in open habitat (e.g., by electrofishing or various net-based methods) similarly may vary in relation to these same factors, such as BONY preference for moving to greater water depths during daylight. These relationships between BONY swimming behaviors and monitoring effectiveness are also suggested more generally by studies of other native fishes in the Colorado River, including the closely related humpback chub (Bestgen et al. 2007; Rogers et al. 2008; Stone 2010; Van Haverbeke et al. 2013; Yackulic et al. 2018). Conversely, efforts to capture fishes may cause them to flee toward cover, resulting in a bi-directional relationship. For example, as noted in the original CEM report (Braun 2015), juvenile and adult BONY energetically try to leap out of floating pens and actively search for escape routes over, under, around, and through nets (Mueller 2006). Mueller (2006) also notes that BONY "...are easily captured from rearing ponds using recreational angling equipment. However, once a fish is hooked, it then becomes difficult to capture others, suggesting the fish

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may release fright pheromones.” 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 BONY. However, link spatial and temporal scale ratings are hypothesized to be high because the relationship should apply wherever and whenever BONY monitoring takes place. *Applies to all life stages except Eggs and Early Larvae.*

- Thermal Stress (CAP) effects on new “... Growth” life-stage outcome for Eggs and Early Larvae, Fry and Juveniles, Newly Stocked Adults, and Established Adults life stages: These links recognize that chronic thermal stress can inhibit BONY 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 high, but the link spatial and temporal scale ratings are estimated to be low: Chronic thermal stress is a commonly recognized cause of impaired body condition and growth in fishes. However, BONY in the river, impoundments, and isolated ponds of the LCR ecosystem face few or no situations in which they experience chronic thermal stress. Correspondingly, link predictability and understanding are both 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 [n = 5 links] on Established Adult Reproductive Participation: These links are replaced with links from these causal agents to Established Adult Growth, as described above, and an added link from Established Adult Growth to Established Adult Reproductive Participation, as described below. *Applies to Established Adults only.*
- Effects of Predation on Established Adult Reproductive Participation [n = 1 link]: This link is no longer needed because Predation affects Established Adult Survival, and this update adds a link from Established Adult Survival to Established Adult Reproductive Participation, as described below. *Applies to Established Adults only.*

- Effects of Predation on Spawning Adult Fertility [n = 1 link]: This link is no longer needed because Predation affects Spawning Adult Survival, and this update adds a link from Spawning Adult Survival to Spawning Adult Fertility, as described below. (Note that the model retains links from Chemical Stress, Disease, Foraging, Mechanical Stress, and Thermal Stress to Spawning Adult Fertility because these are direct effects of stress, not mediated by a “Growth/Condition” LSO). *Applies to Spawning Adults only.*

UPDATED LINKS WITH CRITICAL ACTIVITIES/PROCESSES AS CAUSAL AGENTS

- Alongside the above new linkages from “...growth” to the five listed critical activities or processes, the CEM retains the original causal linkages from these five critical activities or processes—Chemical Stress, Disease, Foraging, Mechanical Stress, and Thermal Stress—to the “...Survival” outcomes for *all five life stages except Spawning Adults, with Foraging also not applicable to Eggs and Early Larvae*. 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 Juvenile Growth, Newly Stocked Adult Growth, and Established Adult Growth (new LSOs) for all three life stages: BONY adult vulnerability to predation may depend, in part, on body size, as discussed in the original CEM. Bestgen et al. (2017) note, “The effects of [BONY] size at stocking into the upper Colorado River are the focus of ongoing analyses, as larger fish may survive at higher rates (Badame and Hudson 2003; Nesler et al. 2003; Zelasko et al. 2010).” Size depends on growth, and 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 larvae, juveniles, and

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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. The hypothesized link accordingly is proposed to be negative, with no known threshold, and unidirectional. Link intensity is unknown, but the link spatial and temporal scales ratings are estimated to be high: The intensity of this relationship is not presently known and is not presently a subject of study by the LCR MSCP (LCR MSCP 2017). 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 BONY have a slender body form. Unlike some other native fishes of the Colorado River Basin, BONY develop only a slight dorsal keel as adults (USFWS 2002), which would have only mildly discouraged pikeminnow predation and only among BONY longer than 200 mm TL (Portz and Tyus 2004; Franssen et al. 2007). Correspondingly, link predictability is unknown and link understanding low. *Applies to Fry and Juveniles, Newly Stocked Adults, and Established Adults only.*

- “... Growth” life-stage outcome effects on swimming (CAP): Links are added from Fry and Juvenile Growth, Newly Stocked Adult Growth, and Established Adult Growth (new LSOs) for all three life stages. The idea here is that growth results in a greater ability to flee or to avoid potentially harmful conditions, as indicated in studies of swimming performance that show greater strength with greater body size. Evidence from studies by Chandos (2017) and Moran et al. (2016), together with the basic concepts underlying the use of Fulton’s condition factor (Froese 2006; Nash et al. 2006) in fact do suggest that BONY swimming performance likely varies with body condition; however, the evidence is limited. The hypothesized link accordingly is proposed to be positive, with no known threshold, and unidirectional. Link intensity is high, but the link spatial and temporal scale ratings are estimated to be low: BONY swimming performance likely varies with body condition. However, adult BONY in the river, impoundments, and isolated ponds of the LCR ecosystem appear to survive for only a few weeks at most before becoming food for some predator, and mostly do not disperse significantly from release sites, limiting the spatial extent and timespan across which this relationship can play out; BONY are not recruiting in these non-hatchery environments; and the LCR MSCP does not release BONY fry or juveniles from the hatcheries. Link predictability and understanding are high. *Applies to Fry and Juveniles, Newly Stocked Adults, and Established Adults only.*
- “... Growth” life-stage outcome effects on “... survival” outcomes: Links added from *Egg and Early Larval Growth, Fry and Juvenile Growth, Newly Stocked Adult Growth, and Established Adult Growth (new LSOs) to Egg and Early Larval Survival, Fry and Juvenile Survival, Newly*

Stocked Adult Survival, and Established Adult Survival, respectively. For the eggs and early larvae, the idea here is that the longer the duration of the life stage (due to slower growth), the longer the eggs and early larvae 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, for example, as suggested by Bestgen et al. (2017). The hypothesized link is proposed to be positive, with no known threshold, and bi-directional: Longer survival reciprocally permits greater growth. Link intensity is high, but the link spatial and temporal scale ratings are estimated to be low: The relationship should be strong, based on core biological principles, but the present system provides few opportunities for the relationship to play out. Adult BONY released into the river and its impoundments and connected backwaters of the LCR ecosystem appear to survive for only a few weeks at most before becoming food for some predator, and mostly do not disperse significantly from release sites, limiting the spatial extent and timespan across which this relationship can play out; BONY are not recruiting in these non-hatchery environments; and the LCR MSCP does not release BONY fry or juveniles from the hatcheries. Isolated ponds such as CHLP and the IPCA ponds, on the other hand, do provide opportunities for the relationship to play out, but these are spatially small scale. Link predictability and understanding are high. *Applies to all life stages except Spawning Adults.*

- Established Adult Growth (new LSO) effect on Established Adult Reproductive Participation (LSO): A link is added between these two life-stage outcomes, with Established 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. Osborne and Turner (2017) have found that the larger females stocked into isolated, protected ponds tend to produce more offspring, but they did not find any similar relationship among the males. The hypothesized link is proposed to be positive, with no known threshold, and unidirectional. Link intensity is high, but the link spatial and temporal scale ratings are estimated to be low: The relationship should be strong, based on core biological principles, but the present system provides few opportunities for the relationship to play out. Adult BONY released into the river and its impoundments and connected backwaters of the LCR ecosystem appear to survive for only a few weeks at most before becoming food for some predator, and mostly do not disperse significantly from release sites, limiting the spatial extent and timespan across which this relationship can play out. BONY do spawn in

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backwaters disconnected from the main stem waters, as studied by Osborne and Turner over many years (2014–16), but these are Newly Stocked Adults temporarily protected from aquatic predators, with body condition governed by hatchery management rather than by in situ growth. Condition data are not available for the BONY used in these experiments (Osborne 2018, personal communication) and would likely not be informative since, as noted, they are controlled by hatchery management and also by the methods used to select BONY for release. Isolated ponds such as CHLP and the IPCA ponds, on the other hand, do provide opportunities for the relationship to play out, but these are spatially small scale. Link predictability and understanding are high. *Applies to Established Adults only.*

- Established Adult Survival (LSO) effect on Established Adult Reproductive Participation (LSO): A link is added between these two life-stage outcomes, with Established Adult Survival as the causal agent. The idea here is that only adults that survive can participate in reproduction (i.e., adults that do not survive do not participate in reproduction). The hypothesized link is proposed to be positive, with no known threshold, and unidirectional. Link intensity and both the link spatial and temporal scale ratings are all estimated to be high: Adult BONY released into the river and its impoundments and connected backwaters of the LCR ecosystem appear to survive for only a few weeks at most before becoming food for some predator, mostly do not disperse significantly from release sites, and do not spawn. Isolated ponds such as CHLP and the IPCA ponds, on the other hand, do have established adults, and these do spawn. Link predictability and understanding are high. *Applies to Established Adults only.*
- 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 (i.e., spawning adults that do not survive do not contribute to fertility in that spawning cycle). The hypothesized link is proposed to be positive, with no known threshold, and unidirectional. Link intensity and both the link spatial and temporal scale ratings are all estimated to be high: Adult BONY released into the river and its impoundments and connected backwaters of the LCR ecosystem appear to survive for only a few weeks at most before becoming food for some predator, mostly do not disperse significantly from release sites, and they do not spawn even if ripe and attempting to participate. Isolated ponds such as CHLP and the IPCA ponds, on the other hand, do see some spawning. Link predictability and understanding are high. *Applies to Spawning Adults only.*

SUMMARY OF STANDARDIZATION OF TERMS

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

Table 4.—(New table for this update): Updated BONY conceptual ecological model component names

BONY conceptual ecological model updated terms, 2018	BONY conceptual ecological model original terms, 2015
Life stages	
<i>(No changes to any life stage names)</i>	
Life-stage outcomes	
Egg and Early Larval Survival	Egg and Early Larval Survival Rate
Egg and Early Larval Growth	(new)
Fry and Juvenile Survival	Fry and Juvenile Survival Rate
Fry and Juvenile Growth	(new)
Newly Stocked Adult Survival	Newly Stocked Adult Survival Rate
Newly Stocked Adult Growth	(new)
Established Adult Survival	Established Adult Survival Rate
Established Adult Growth	(new)
Established Adult Reproductive Participation	Established 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	(new)
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
Post-Rearing Transport and Release	Post-Rearing Transport and Release Methods
Pre-Release Conditioning	Pre-Release Conditioning
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	
BONY Monitoring and Conservation Programs	Augmentation Program Operations
Channel and Off-Channel Engineering	Channel, Lake, Pond Design and Operations
Motorboat Activity	Motorboat Activity
Non-BONY 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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