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ARTICLE

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Abstract
We developed an individual-based population viability analysis model (females only) for evaluating risk to populations from catastrophic events or conservation and research actions. This model tracks attributes (size, weight, viability, etc.) for individual fish through time and then compiles this information to assess the extinction risk of the

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population across large numbers of simulation trials. Using a case history for the Little Colorado River population of Humpback Chub *Gila cypha* in Grand Canyon, Arizona, we assessed extinction risk and resiliency to a catastrophic event for this population and then assessed a series of conservation actions related to removing specific numbers of Humpback Chub at different sizes for conservation purposes, such as translocating individuals to establish other spawning populations or hatchery refuge development. Our results suggested that the Little Colorado River population is generally resilient to a single catastrophic event and also to removals of larvae and juveniles for conservation purposes, including translocations to establish new populations. Our results also suggested that translocation success is dependent on similar survival rates in receiving and donor streams and low emigration rates from recipient streams. In addition, translocating either large numbers of larvae or small numbers of large juveniles has generally an equal likelihood of successful population establishment at similar extinction risk levels to the Little Colorado River donor population. Our model created a transparent platform to consider extinction risk to populations from catastrophe or conservation actions and should prove useful to managers assessing these risks for endangered species such as Humpback Chub.

Historically, Humpback Chub *Gila cypha* in Grand Canyon were thought to be widely distributed with spawning populations in both the main-stem Colorado River and several tributary systems (Ryel and Valdez 1995, observations summarized in Webb et al. 2002). Since the completion of the Glen Canyon Dam (GCD) in 1963 and the filling of Lake Powell upstream of Grand Canyon, water temperatures in this river reach have generally been considered too low for spawning and successful recruitment of Humpback Chub (Hamman 1982a; Kaeding and Zimmerman 1983). Currently only one tributary, the Little Colorado River, is known to support Humpback Chub spawning and rearing (Gorman and Stone 1999), and efforts are ongoing in three other tributaries (Shinumo, Havasu, and Bright Angel creeks) to evaluate their potential as translocation sites (Trammell et al. 2012). Other aggregations of adult and juvenile fish are found at several locations in the main stem, with most associated with tributary inflows (Ryel and Valdez 1995; Paukert et al. 2006). There is little evidence of successful recruitment outside of the Little Colorado River (Valdez and Masslich 1999; Andersen et al. 2010), and tagging data suggest that most fish originate as dispersers from the Little Colorado River (i.e., they are "sink" populations [Paukert et al. 2006]). Juveniles and adults from the Little Colorado River population continue to use the Little Colorado River and main stem seasonally.

Humpback Chub populations have declined from historical levels, and the risk of extinction is sufficient to warrant listing under the U.S. Endangered Species Act (ESA; Coggins et al. 2006). Three primary reasons for the decline of Humpback Chub populations in Grand Canyon are widely considered, including (1) negative interactions with nonnative fish (Coggins et al. 2011; Yard et al. 2011), (2) loss of essential habitats following flow modifications post-GCD (Converse et al. 1998; Stone and Gorman 2006), and (3) temperature changes in the main-stem river due to cold, hypolimnetic releases from GCD (Hamman 1982a; Clarkson and Childs 2000). After a period of decline through the 1980s and 1990s, the Little Colorado River population has shown increased recruitment since at least 2002 and now appears to have stabilized at a relatively large population of 6,000–9,000+ adults (Coggins et al. 2006; Coggins and Walters 2009). However, these increases have occurred in conjunction with efforts to control exotic predators (mainly trout [family Salmonidae]) and with increased water temperatures associated with low reservoir levels in Lake Powell (Coggins et al. 2011). Climate conditions driving reservoir water levels, hydrology, and water deliveries that control riverine water temperatures (Pulwarty and Melis 2001) are increasingly uncertain as are management options to control nonnative fish. Coupled with increasing uncertainty over future water resource development projects in key tributary systems such as the Little Colorado River from mining and other water use projects, these (and other) risks to Humpback Chub in Grand Canyon persist.

Our knowledge of juvenile Humpback Chub population ecology is much sparser than for adult life stages. Based on our collective experiences, the current paradigm for juveniles suggests that (1) there is some evidence of strong density dependence in survival rates of juveniles rearing in the Little Colorado River, (2) there is little apparent relationship between age-2 recruitment reconstructed from PIT tag data and estimated adult abundance, and (3) strong age-1 juvenile cohorts are seen in hoop net sampling roughly every other year, but by age 2 these cohorts are typically no more abundant than fish from less abundant age-1 cohorts. As an example, Ryel and Valdez (1995) tracked one particularly strong cohort (1993) and suggested it suffered much higher dispersal and mortality rates, along with relatively poor growth, than surrounding cohorts. These observations are key to developing an effective translocation strategy because if juvenile mortality rates are indeed strongly density dependent, with the Little Colorado River being "filled to rearing capacity" every year, then it may be possible to remove substantial proportions of the Little Colorado River juveniles for transplants and scientific study without endangering the Little Colorado River population. If there is similar density dependence in juvenile survival rates of fish transplanted to and spawned in other tributaries, extinction risks for these tributaries will be much lower than would be predicted from the small adult population sizes likely to develop in them.

To minimize extinction risks, management agencies have adopted a series of goals and actions to conserve this species, including translocation of Humpback Chub to tributaries to the Colorado River in Grand Canyon (USFWS 2008, 2011) and hatchery-based refuge populations (USFWS 2008, 2011). Specifically, the 1995 Biological Opinion on the operation of GCD included the establishment of a second aggregation of Humpback Chub downstream of GCD as a Reasonable and Prudent Alternative, and the 2011 Biological Opinion calls for coordinated efforts to "expand the role of tributaries and their ability to contribute to the growth and expansion of main-stem aggregations" (USBOR 1995; USFWS 2011). Additionally, to address key research needs on early life history of Humpback Chub, there is increased interest in allowing permitted take of a very small number of fish for research purposes (i.e., otolith analyses) as well as better quantifying the risks to the population due to incidental mortalities from sampling (USFWS 2011; Hunt et al. 2012). The Little Colorado River population is seen as a potential source of juvenile fish for translocations or permitted take for scientific study. Conservation measures from the 2011 Biological Opinion (USFWS 2011) will require juvenile translocation of Humpback Chub from the Little Colorado River on an annual basis (Valdez et al. 2000) to augment tributary populations in Grand Canyon and maintain refuge populations. This strategy could have impacts to the source population in the Little Colorado River as well as an unknown potential for success in tributaries targeted for translocations (USFWS 2010, 2011). Thus, using a model to screen risks to the Little Colorado River population and inform translocation strategies would benefit managers in balancing conservation measures with risks to the sustainability of source populations and the likelihood of success of target populations.

For a wide range of management scenarios, quantitative population viability models can be used to evaluate the likelihood of populations approaching size or vital rate thresholds deemed critical to continued species persistence (National Research Council 1995; McGowan and Ryan 2009, 2010). Quantitative models are beneficial because their founding assumptions are transparent and, owing to their probabilistic origins, the uncertainty of predictions are readily quantified and can be incorporated into the decision-making process (Hilborn and Mangel 1997). Despite the applicability associated with this approach, few examples of ESA-engendered questions or risk assessments are available in the literature.

We developed an individual-based population model for evaluating extinction risk to the Little Colorado River Humpback Chub population through the collection of individuals for ESA-mandated conservation purposes (refuge establishment, translocations, permitted take) and also to assess the likelihood that populations can be established in tributaries outside the Little Colorado River. Specifically, we use the model to evaluate the following: (1) What is the current extinction risk for the Little Colorado River population and is it resilient to a catastrophic event? (2) What proportion of the Little Colorado River juvenile population, and at what sizes or ages, can be removed without increasing extinction risk to the Little Colorado River population? (3) Given that other tributaries may have lower juvenile rearing capacities and potential adult population sizes than the Little Colorado River, how likely are they to go extinct due to demographic stochasticity, so as to require continuing translocations from the Little Colorado River for permanent establishment? Finally, given 1–3 above, what translocation strategies are most appropriate to achieve a successful second population?

METHODS

Individual-based models (IBMs) are widely used in ecology (DeAngelis and Mooij 2005), often for small populations. Their benefits include the following: (1) population attributes (i.e., recruitment, mortality) are described with distributions rather than mean values, (2) individual animals are explicitly tracked, which is the scale that drives population dynamics, and (3) results are expressed as the sum of characteristics of the individual survivors (DeAngelis and Rose 1992; Letcher et al. 1998). The model allows entry and saving of population dynamics parameters, and "running the model" consists of simulating multiple replicate population histories each with random survival events over time for each individual fish. The model also assumes random variation in juvenile survival rates associated with environmental factors likely to cause variation in such rates. An IBM can also represent density-dependent survival patterns of juveniles over multiple juvenile "stanzas" representing distinct ontogenetic habitat-use patterns and juvenile size–age ranges, which allows for testing of sensitivity to stanza complexity. Finally, the IBM can run large numbers of stochastic simulations quickly to allow rapid screening of policy options and sensitivity analysis of the results to uncertainties about key population parameters.

The Individual-Based Population Model

In the model we developed, each individual-based simulation trial begins by constructing a list of N_o individual female fish, $i = 1, 2, \ldots, N_o$. Each fish i is assigned an initial age a_i based on an assumed initial stable age distribution calculated from age-specific survival rates $S(a)$ (with a standard deviation of 0.5 on age-0 survival). For each simulated year $t = 1,2,.,t$, each individual either becomes a year older or dies between year t and t_{+1} and is removed from the list with probability 1-$S(a_i)$. The population in year t is just the sum of the surviving population N_t. These random individual choices result in simple "demographic stochasticity" in age-1 and older abundance.

Total larvae production E_t for each year t is calculated from the surviving individuals as a sum over individuals of age-specific fecundities, i.e.,

$$E_t = \sum_{i=1}^{N_t} F(a_i). \tag{1}$$

The age-specific fecundity relationship $F(a)$ is assumed to be fixed over time, and is calculated by assuming that fecundity is linearly proportional to body weight at age minus weight at maturity w_{mat}, where weight at age $w(a)$ is assumed to follow the von Bertalanffy relationship

$$w(a) = [1 - e^{-K_a}]^3. \quad (2)$$

Here, K is the von Bertalanffy metabolic coefficient. For ages such that $w(a) > w_{mat}$, $F(a)$ is given by

$$F(a) = f[w(a) - w_{mat}], \quad (3)$$

where f is an estimate of larvae per unit relative weight.

The real heart of our simulation is in determining the fates of the E_t larvae for each year. Larvae that survive their first year are added with age $a_i = 1$ to the list of older fish for the next simulated year. Larvae survival to age-1 is predicted using a multistanza Beverton–Holt stock–recruitment relationship that allows for density dependent survival rates during each stanza and for random "environmental effects" on survival. The deterministic form of the average larvae to age-1 recruitment relationship is assumed to be

$$N_1 = \frac{AE_t}{1 + BE_t}. \quad (4)$$

Here, A is maximum survival rate at low larvae densities, and B represents the strength of density effects that lead to maximum possible recruitment A/B at very high E_t. As noted by Beverton and Holt (1957) in their original derivation, and later by Moussalli and Hilborn (1986), this overall form of relationship is maintained when fish in fact pass through multiple juvenile stanzas $s = 1, \ldots, S$, where survival through each stanza follows the same form as equation (4) with maximum survival rate and density dependence parameters A_s, B_s. The overall parameters A, B are then given by

$$A = \prod_{s=1}^{S} A_s \quad (5)$$

$$B = \sum_{s=1}^{S} \left[B_s \prod_{s'=0}^{s'=s-1} A_{s'} \right] \; (A_0 = 1). \quad (6)$$

The "compensation ratio" (CR) parameterization (Walters and Martell 2004) is used where

$$A = \frac{CR}{EPR_o} \quad (7)$$

$$B = \frac{CR - 1}{(Ro)(EPRo)}. \quad (8)$$

The CR is the Goodyear compensation ratio (of maximum survival rate to survival rate at average size R_o) and EPR_o is average larvae production per age-1 and older individual. There is rarely data to allow direct estimates of stanza-specific A_s, B_s, so we specify alternative hypotheses about the distribution of survival and density effects over each life history stanza (Table 1). This is done by specifying mortality rates M_s^* and density effect B_s^* for each life history stanza relative to each other (Walters and Martell 2004). The A_s and B_s are calculated from these hypothesized relative rates using

$$A_s = e^{\frac{\ln(A) M_s^*}{\sum M_s^*}} \quad (9)$$

$$B_s = B_s^* \frac{B}{\sum_{s'} B_{s'}^* \prod_{s''=0}^{s''=s'-1} A_{s''}}. \quad (10)$$

These scales and conversion formulas are used to assure that the by-stanza parameters A_s, B_s are scaled so that their overall mean prediction across stanzas follows the overall A, B relationship of equation (4).

"Environmental" variation in maximum survival rates A_s is simulated by assuming lognormal variation in these rates, so that the stanza-specific rate A_{st} for each year is given by:

$$A_{st} = A_s e^{W_{st}}. \quad (11)$$

Here W_{st} is a year- and stanza-specific normal random deviate, with mean 0 and standard deviation σ_s. The assumption of independent values of these deviates across stanzas ignores possible correlation across stanzas in impact of factors such as flooding and flow-related changes in habitat area. The population viability impacts of such correlations can be simulated simply by increasing the assumed standard deviation of the W_{st}.

Recruitment for each year is simulated in our model by starting with the E_t individual larvae computed for that year, then simulating survival of these individuals through each of the stanzas by assuming each live individual at the start of each stanza has stanza-specific survival rate

$$S_{st} = \frac{A_{st}}{1 + B_s N_{st}}. \quad (12)$$

Here, $N_{st} = E_t$ for stanza 1, and for $s > 1$ is the number of individual survivors from a previous stanza ($s-1$). Each of final number of recruiting individuals (i.e., individuals surviving the final stanza S), N_{St}, is added to the list of live individuals N_i and assigned age $a_i = 1$, in preparation for beginning the next simulation year.

To simulate removal of juveniles for sampling and transplant policies, the A_{st} values were modified as "harvest rates" h_{st} for each stanza, in which case A_{st} in equation (12) is multiplied by $(1-h_{st})$ before applying the modified S_{st} to the individuals entering stanza s. Likewise, to simulate transplants into a population, the stanza entry numbers N_{st} can be modified upward by year- and stanza-specific stocking rates TP_{st} (absolute number of fish transplanted or stocked into the population) before survival rates for the stanza are applied.

TABLE 1. Input parameter estimates and sources for Humpback Chub in Grand Canyon. Input parameter estimates with high uncertainty are marked in bold italics.

Model parameter	Estimate	Source
Initial age-1 and older female population size (N_o)	3,000 for Little Colorado River, zero for other tributaries	Population estimates for Little Colorado River and Colorado River (Van Haverbeke et al. 2011; Coggins and Walters 2009)
Age-1 and older female Humpback Chub carrying capacity estimates (N_o)	3,000 for Little Colorado River 104–156 age 1 and older (small capacity) 291–437 age 1 and older (medium capacity) 2,000–2,500 age 1 and older (high capacity)	Mark–recapture in Little Colorado River (Van Haverbeke et al. 2011); guessed for smaller tributaries based on relative habitat area
Average long term age-1 recruitment (R_o)	1,500–2,500	Mark–recapture in Little Colorado River (Van Haverbeke et al. 2011); guessed for smaller tributaries based on relative habitat area
Recruitment compensation ratio (CR)	***2.0*** or ***4.0***	Average from stock–recruitment meta-analyses (Myers et al. 1999; Goodwin et al. 2006)
Annual survival rates of age-1 and older fish	0.4 for age 1 0.65 for age 2 0.86 for age 3 and older	Ratios of fish age 1–2 in closed mark–recapture (Van Haverbeke et al. 2011); ASMR fitting to PIT tag recovery data (Coggins et al. 2006; Coggins and Walters 2009) for age 2 and older
VonBertalanffy growth (K)	0.14	Estimated from PIT tag growth rates (Coggins and Walters 2009)
Length at maturity–maximum length, implies weight at maturity (w_{mat})	0.5	Gives maturity at 4–5 years (Ryel and Valdez, 1995)
Larvae produced per body weight of spawners (f)	***600***	Based on single fecundity estimate of 2,523 (Hamman 1982a) $\times$ 0.1 egg to larvae survival
Relative mortality rates of juvenile stanzas (M_s^*)	Larvae <30 mm: ***3.0*** Larvae 30–60 mm: ***2.0*** Juveniles 60–80 mm: ***1.0*** Large juv. 80–130 mm: ***0.8***	Assumes M decreases linearly with length (Lorenzen 2000)
Relative density dependence in mortality by stanza (B_s^*)	Larvae <30 mm: ***5.0*** Larvae 30–60 mm: ***2.0*** Juveniles 60–100 mm: ***1.0*** Large juveniles 80–130 mm: ***1.25***	Assumes density effect decreases with increasing size, no direct data
Standard deviation of environmental effect on survival (σ_e)	0.50 per stanza for all of age 0–1.5	Standard deviation of log age-1 abundance estimates from mark–recapture

In summary, the input data consists of the following:

(1) an assumed initial population size N_o and a population size estimate at carrying capacity;
(2) age-specific but time-independent survival probabilities $S(a)$ for recruited (age-1 and older) individuals, assumed for parameter entry convenience to be the same for ages $a = 3$ and older;
(3) growth-fecundity parameters K, w_{mat}, and f;
(4) the recruitment scale and compensation parameters R_o, and CR needed to calculate overall Beverton–Holt parameters A and B (EPR_o is calculated from the age-fecundity relationship and average survivorship from the $S(a)$ rates), noting that R_o determines average long-term population size, which can differ considerably from the initial population size N_o;
(5) stanza-specific relative juvenile survival and density effect parameters M_s^* ,B_s^* ;
(6) the standard deviation(s) for lognormal environmental effects on stanza survivals, σ_e; and
(7) management policy parameters, namely the juvenile stanza-specific harvest–transplant removal rates h_{st} and stocking

rates TP_{st} (harvest rates of older fish can also be represented by reducing the annual survival rates $S(a)$.

Note that changes in the survival rate and management policy removal parameters can also be used to simulate other changes that might affect juvenile survival rates, such as invasions by exotic warmwater or coldwater predators, emigration of fish from translocation sites, or harvesting of older fish. Also, N_o can be set very low compared to the expected average long-term population size given approximately by $R_o/(1–S_{adult})$, to explore the risk of extinction following some catastrophic mortality event that leaves only N_o survivors.

Estimation of Recruitment and Survival Parameters

Mark–recapture data provide direct estimates of many of the model inputs for the Little Colorado River Humpback Chub population, and other inputs used have been approximated or inferred from published meta-analyses (Table 1). In assembling input parameter estimates, we were surprised at how low the published estimate of fecundity for Humpback Chub was (mean = 2,523 eggs/female, range = 330–5,445, $N = 8$; Hamman 1982a) relative to the closely related Bonytail *G. elegans* (mean = 25,090 eggs, range = 5,850–37,700 eggs, $N = 5$; Hamman 1982b) and Roundtail Chub *G. robusta* (mean = 18,699 eggs, range = 13,816–26,903 eggs, $N = 5$; Brouder et al. 2006). This fecundity estimate is critical, since it determines the initial number of larvae entering the multistanza density-dependent calculation and hence the overall juvenile survival rates A_s needed to result in observed numbers of age-1 recruits. Increasing assumed fecundity results in reduced A_s survivals and a dampened impact of early stanza harvest rates h_{st}.

There is no direct way to estimate the critical recruitment compensation ratio *CR* from Grand Canyon Humpback Chub population data; the historical data span too narrow a range of adult abundances to allow direct assessment of relative recruitment success at very low population densities compared to juvenile production at higher population size. After reviewing estimates for stream- and lake-rearing Pacific salmon (Coho Salmon *Oncorhynchus kisutch* and Sockeye Salmon *Oncorhynchus nerka* [Myers et al. 1999]) that undergo similar ontogenetic habitat shifts and likely changes in predation risk we used a *CR* value of either 2 or 4. In our simulations a value of 2 would be considered very conservative and a value of 4 a less conservative approach to compare policy options. The maximum by-stanza survival rates A_s implied by the M_s^* values in Table 1 are quite reasonable given the high likelihood that mortality rates M_s are strongly size dependent as in other fish species (Lorenzen 2000). However, closed (Petersen) mark–recapture estimates for age-1 and age-2 juveniles in the Little Colorado River are apparently not strongly correlated (R. VanHaverbeke, unpublished), suggesting the possibility of a higher compensation ratio and stronger compensation for older juveniles than assumed in the base B_s^* values in Table 1. Intensive mark–recapture programs have been conducted almost annually in the Little Colorado River and adjacent Colorado River main stem since the early 1990s, such that most Humpback Chub in that tributary are now PIT-tagged by the time they reach 5–7 years of age and they are repeatedly sampled over their long life of 30 + years with annual survival of about 85% (Coggins et al. 2006). This sampling program has provided key demographic information on survival rates and recruitment, along with relatively precise estimates of population size and trend (Coggins et al. 2006; Coggins and Walters 2009) over this time period.

Modeled Scenarios

Scenario 1: Extinction risk and recovery of the Little Colorado River population following a catastrophic mortality event.—The Little Colorado River population of Humpback Chub is the largest known (Meretsky et al. 2000), and likely about 73% of all remaining Humpback Chub rangewide (3,300 adults in the upper Colorado River basin versus 6,000–9,000+ adults in Grand Canyon; Coggins et al. 2006; Coggins and Walters 2009) spawn successfully in this one tributary system. Given the critical conservation importance of this one tributary system there is concern among management agencies (USBOR 1995; USFWS 2008) about some sort of catastrophic event from spills, runoff from mining, or forest fire within the basin (e.g., hazardous materials spill from the Highway 89 bridge located 55–65 km upstream). This type of event could cause a singular large mortality similar to the sodium hydroxide spill on the Cheakamus River in British Columbia (BCME 2006). We estimated extinction probability by assuming that 95% of the Humpback Chub stock was eliminated (reduction in the number of females from 3,000 to 150) and then simulated the population recovery over a 200-year period 1,000 times using a base *CR* value of 4 and again using the more conservative *CR* value of 2.

Scenario 2: Assessing risk to the Little Colorado River donor population.—Removal of Humpback Chub from the Little Colorado River population for any reason must be carefully considered so as to not increase the extinction risk of the population (USFWS 2008). For both research and translocation purposes, larvae and juvenile size-classes of Humpback Chub are those most often considered for permitted take from the Little Colorado River. But at what removal levels would removal increase the extinction risk to the Little Colorado River population? Humpback Chub spawn in the Little Colorado River primarily in March and April and juveniles first recruit to standard sampling gear in early summer and remain present throughout the summer, fall, and overwinter (Kaeding and Zimmerman 1983; Gorman and Stone 1999). Catch of these juveniles is highly dependent on river discharge and turbidity (Stone 2010) with annual catch ranging from 10s to 1,000s of fish in these size-classes. The Little Colorado River Humpback Chub population requires recruitment levels of about 2,700–2,900 recruits per year to have a basically stable population size. We assessed the risk to the Little Colorado River population by modeling removals of 10–50% of the Humpback Chub recruits in four size categories ranging from larvae (<30 mm TL) to three size categories of juveniles (30–60 mm TL, 60–80 mm TL, and 80–130 mm TL). For each of these scenarios we assessed a small removal of 10% of each size-class and a large removal of 50% of each size-class for a 5-year period, assessed the yield of fish in the last year of the removal (number cropped), the extinction risk to the population following removal, and then monitored the population recovery over an additional 5-year period. For each cropping level, this 10-year time period was repeated 1,000 times. We compared the extinction risk in each removal scenario to the base case of no removals (with extinction risk = 0) as well as the resulting age-1 and older abundance at the end of the 10-year simulation with the base case. We also assessed how sustained removals of 10% of the larvae or 50% of the large juveniles for a 200-year period would impact the Little Colorado River population of Humpback Chub by comparing these sustained removals to baseline simulations with no removals.

Scenario 3: Informing translocation strategies.—Scenario 3 focuses on informing translocation policies by assessing tradeoffs in size-class and number of fish stocked into a tributary stream from the donor population (USFWS 2008). The goal was to identify stocking policies that have a high probability of establishment (>90%, equivalent to a risk of extinction <10%) over a 50-year time period. This was done by iteratively stocking varying numbers of fish (females) into the donor streams for five consecutive years until the probability of establishment over a 50-year time period met the success criteria above. We identified numbers and size-classes of Humpback Chub stocked that would be necessary to result in an extinction risk of <10% over 50 years with translocations initially occurring for five consecutive years. We assessed stocking using the same four size-classes identified above. We also evaluated how a higher emigration rate or predation rate of 40% of age-1 translocated fish would affect the establishment rate.

The recipient streams are other tributaries outside of the Little Colorado River (i.e., Havasu, Shinumo, and Bright Angel creeks) that are considerably smaller in discharge than the Little Colorado River but currently do not support Humpback Chub populations either because of geographic barriers to migration or high abundances of predatory nonnative species (e.g., Rainbow Trout *Oncorhynchus mykiss* or Brown Trout *Salmo trutta* in Bright Angel Creek, Omana-Smith et al. 2012). Based on our current knowledge of Humpback Chub ecology and knowledge of the flow, temperature, substrate and invertebrate production (Oberlin et al. 1999) in these streams, they are likely suitable for hosting reproducing Humpback Chub populations.

In this scenario, we first had to calculate the potential female Humpback Chub carrying capacity of each recipient stream which would provide reasonable upper bounds for population growth (Table 1). Since these limiting factors are unknown, as an approximation we calculated the potential carrying capacity of the Little Colorado River using abundance estimates from mark–recapture data and expert opinion on habitat requirements to determine a carrying capacity scaler/m^2 of shoreline habitat. This scaler was then applied to the approximate shoreline area of critical habitat in each tributary system to estimate the potential carrying capacity. We used three carrying capacities (low, medium, and high carrying capacity; Table 1) in tributary streams ranging from about 100–2,500 age-1 and older female fish (tributary characteristics summarized in Valdez et al. 2000). All other assumptions were the same as those calculated for the Little Colorado River and identified in Table 1.

RESULTS

We found that Humpback Chub populations are resilient with low extinction risk from catastrophe or permitted take of larvae or juveniles for research or translocation purposes at proposed levels (e.g., 10s to 100s of fish for stomach content or otolith analyses). Our results suggest that the Little Colorado River population is resilient to some sort of catastrophic event but that recovery following a major mortality event could take 50–100 years. We also found that the potential benefits in terms of expanding knowledge of juvenile Humpback Chub population ecology or establishing spawning populations in other tributaries exceeds the risks to the Little Colorado River population of negative effects following removals for translocation. Finally, we found that if tributary streams are suitable recipients for translocated juvenile Humpback Chub from the Little Colorado River donor population, then these populations have a high probably of establishment and persistence.

Scenario 1: Recovery from Catastrophe

At both the base conservative *CR* of 2 and a *CR* of 4 we predict recovery of Humpback Chub populations following episodic reduction by 95% within approximately 100 years of impact under both scenarios (Figure 1). Risk of extinction within 200 years was zero for both *CR* scenarios evaluated and recovery was more rapid at the higher $CR = 4$ scenarios. As an extreme example, if only 5 female fish (5 of 3,000) survived the catastrophic event then extinction risk increases to between 5% and 8% for a *CR* of 4 and about 22–25% for a *CR* of 2.

Scenario 2: Extinction Risk to Little Colorado River from Removals

We estimated a baseline recruitment level of age-1 fish through simulations with no removals. These baseline levels represent the population of recruits without removal for *CR* values of 2 and 4, and correspond to about 2,900–3,000 age-1 and older female fish each year, respectively (Figure 2A).

Larvae <30 mm TL.—Our results for a *CR* value of 2 and a 10% removal of larvae annually for 5 years results in removal levels of approximately 25,000–26,000 larvae each year and ultimately less than a 1% reduction from the baseline (no removal) level of age-1 and older Humpback Chub after 5 years of recovery following removal (Table 2; Figure 2B). As the removal percentage increased to 50%, this resulted in about 127,000–128,000 larvae a year available for harvest during the

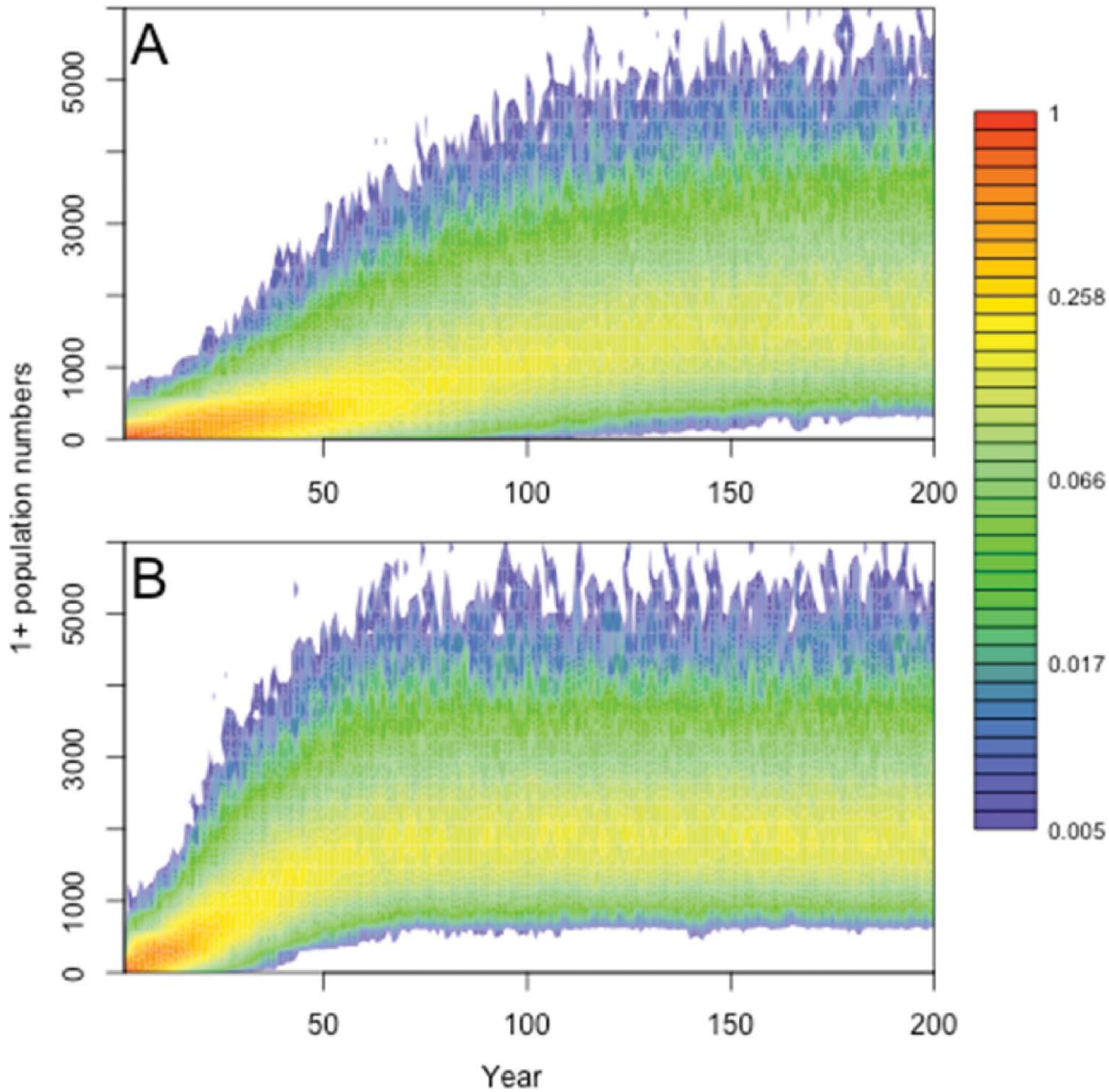

FIGURE 1. Recovery of the Humpback Chub population (age 1 and older) following a 95% reduction in abundance due to a catastrophic event with a recruitment compensation ratio of **(A)** *CR* = 2 and **(B)** *CR* = 4. Red colors indicate higher observation densities and dark blue colors indiciate lower observation densities (indicated in the legend) from the 1,000 replicate simulation trials.

5-year removal period leading to a reduction in age 1+ Humpback Chub of 7.6% 5 years postremoval (Figures 2A, 2C). In comparison, a less conservative *CR* value of 4 would result in a similar yield but smaller population reduction in age-1 and older Humpback Chub of 4.2% (Table 2; Figure 2E). This result of a lower predicted impact to age-1 and older Humpback Chub populations following removals when a higher *CR* was assumed was consistent across all removal levels assessed (Table 2).

Small juveniles 30–60 mm TL.—Assuming a *CR* value of 2, removals of 10% of the small juveniles annually for 5 years yielded about 1,400–1,500 each year and resulted in an estimated reduction in age-1 and older population size of <1% (Table 2) five years postremoval. A higher removal rate of 50% increased the number of small juveniles removed (7,500–8,000) and also reduced age-1 and older Humpback Chub population size by 11.9% 5 years postremoval (Table 2). Using a less conservative *CR* of 4 removals of 50% led to lower yields (5,000–5,500) and not as high a reduction in age-1 and older abundance postremoval period (11%; Table 2)

Medium juveniles 60–80 mm TL.—Removals of medium-sized juveniles annually for 5 years using a *CR* = 2 or 4 were generally similar to the smaller juveniles. Removals of 10% each year for 5 years resulted in 300–350 juveniles for harvest and reduced age-1 and older abundance by about 2% 5 years

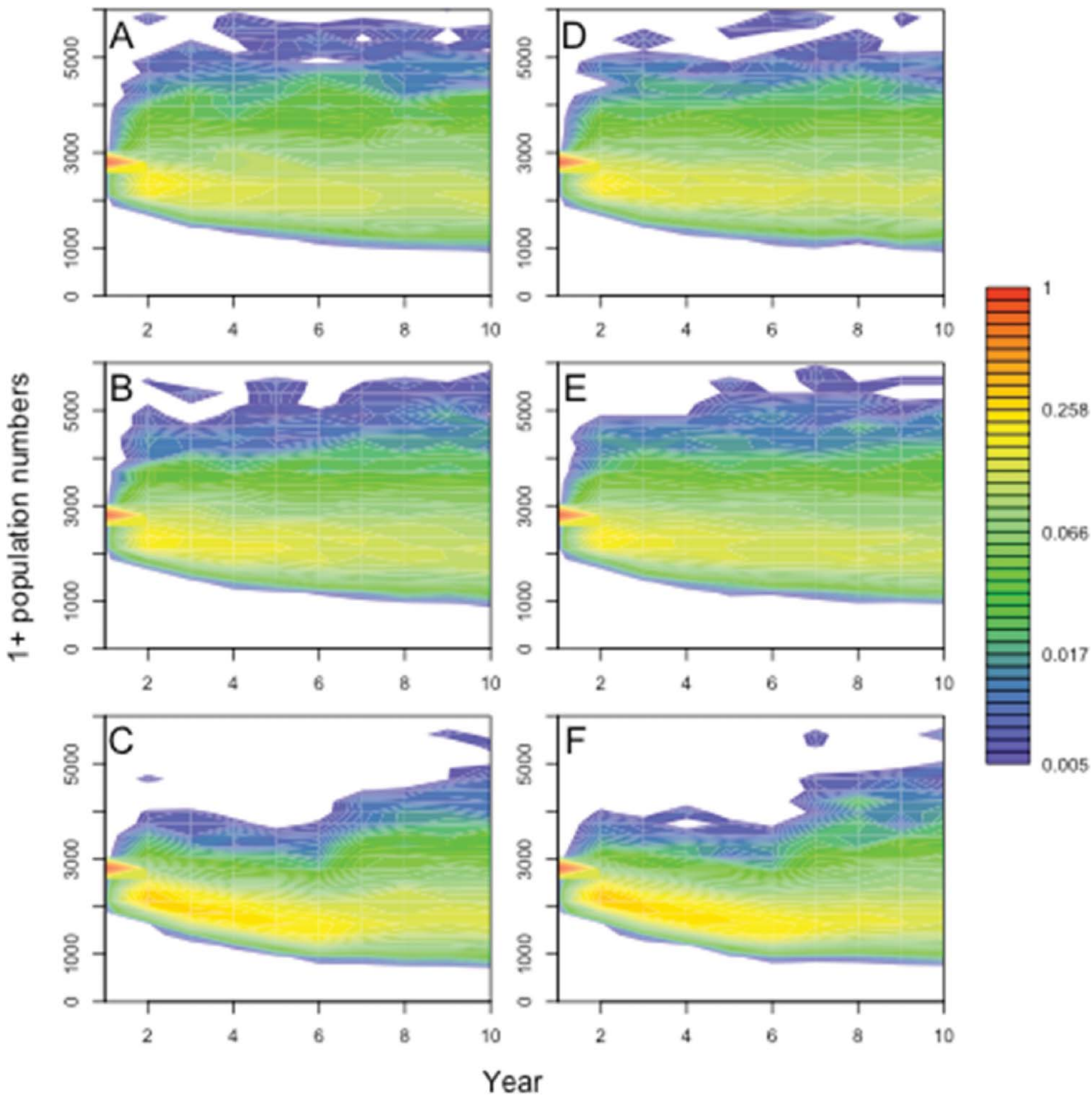

FIGURE 2. Change in Humpback Chub age-1 and older abundance following different cropping scenarios. Panels **(A)** and **(D)** represent a "base" case with no cropping and a compensation ratio (A) $CR = 2$ and (D) $CR = 4$. Panels **(B)** and **(E)** represent 10% annual removal of larvae (<30 mm TL) each year for 5 years and a (B) $CR = 2$ and (E) $CR = 4$ scenario. Panels **(C)** and **(F)** represent 50% removals of large juveniles (80–130 mm TL) each year for 5 years with (C) $CR = 2$ and (F) $CR = 4$. Red colors indicate higher observation densities and dark blue colors indiciate lower observation densities (indicated in the legend) from the 1,000 replicate simulation trials.

postremoval. Increasing the removal rate to 50% per year reduced populations of age-1 and older Humpback Chub by about 14% 5 years postremoval and yield increased to 1,650–1,750 juveniles per year during the removal period. Again, a less conservative $CR = 4$ reduced the age-1 and older population impacts of removing medium-sized juveniles (about 12%) and yield of juveniles available to harvest (1,400–1,450 medium-sized juveniles; Table 2).

Large juveniles 80–130 mm TL.—For a $CR = 2$ removal of 10% of the largest juvenile female Humpback Chub is estimated to yield about 150–200 fish each year during the 5-year removal period and result in <1% reduction in age-1 and older population size 5 years after removal. Increasing the removal rate to 50% per year yielded about 800–850 fish for removal and reduced the population of age-1 and older fish by about 13% 5 years following the end of removals (Figure 2C). Results were similar with a $CR = 4$ yielding about 750–800 large juvenile females available for removal and a reduction in age 1+ abundance by 11% 5 years after the removal period ended (Table 2; Figure 2).

TABLE 2. Scenario 2 results assessing the change in number of age-1 and older Humpback Chub in the Little Colorado River from cropping either 10% or 50% of the available female fish from different size-classes for translocation or research purposes at different recruitment compensation (*CR*) levels for a 5-year period and then monitoring population recovery for a 5-year period. One thousand simulation trials were run for the 10-year simulation. The yield is the average number of fish available for cropping in the last year of the 5-year removal period. The approximate *N* is the number of age-1 and older fish at the end of the 5-year recovery period following the 5 years of cropping.

Case	*CR*	Percent cropped	Approximate *N* age-1 and older range	Approximate percent change in age-1+ and older abundance over base value of no cropping	Approximate yield	Extinction probability
Base	2	0	2,900–3,000	0	0	0
Base	4	0	2,900–3,000	0	0	0
Larvae <30 mm TL	2	10	2,900–2,950	<1%	25,000–26,000	0
Larvae <30 mm TL	2	50	2,700–2,750	7.6%	127,000–128,000	0
Larvae <30 mm TL	4	50	2,800–2,050	4.2%	128,000–129,000	0
Small juveniles 30–60 mm TL	2	10	2,900–2,950	<1%	1,400–1,500	0
Small juveniles 30–60 mm TL	2	50	2,550–2,650	11.9%	7,500–8,000	0
Small juveniles 30–60 mm TL	4	50	2,600–2,650	11.0%	5,000–5,500	0
Medium juveniles 60–80 mm TL	2	10	2,850–2,950	1.7%	300–350	0
Medium juveniles 60–80 mm TL	2	50	2,500–2,600	13.6%	1,650–1,750	0
Medium juveniles 60–80 mm TL	4	50	2,550–2,650	11.9%	1,400–1,450	0
Large juveniles 80–130 mm TL	2	10	2,900–2,950	<1%	150–200	0
Large juveniles 80–130 mm TL	2	50	2,550–2,600	12.7%	800–850	0
Large juveniles 80–130 mm TL	4	50	2,600–2,650	11.0%	750–800	0

Scenario 3: Informing Translocation Strategies

We found consistent patterns in our translocation strategy evaluation where translocation success is equally likely from a policy of stocking larger numbers of small female fish (generally 1,000–1,200 <30-mm-TL female fish per stream per year for 5 years) or stocking fewer numbers of larger-sized female Humpback Chub (15–30 females >60 mm TL per stream per year for 5 years) had similar probability of extinction rates (<10%) over a 50-year time period and a *CR* of 2 (Table 3). At the end of the 50-year simulation period, each stream would be expected to support about 30–90 age-1 and older females, which would represent as much as 28% of a small stream with low carrying capacity or as little as 4% of a stream with larger carrying capacity. This is because larger streams take longer time periods to reach carrying capacity than smaller streams.

DISCUSSION

Our model and case history analysis with Humpback Chub populations in Grand Canyon provides clear guidance on several important regulatory and policy commitments. We provide a transparent framework in which to assess risks to populations from permitted take of an endangered species (McGowan and Ryan 2010). Endangered and threatened species are also provided legal protection under the ESA (as well as similar laws in other countries, i.e., Species at Risk Act in Canada), which provides strict regulation on any purposeful or incidental take of the species or population of concern that may "cause jeopardy" and alter the likelihood of a species survival or recovery. These types of actions are often covered as part of Section 7 consultations under the ESA and included in Biological Opinions required by the U.S. Fish and Wildlife Service for all listed and threatened species (USFWS 2011). Our model and case history example builds on recommendations from National Research Council (NRC 1995) and McGowan and Ryan (2009, 2010) to use population models to evaluate take (incidental or permitted) effects on listed species because it (1) is based on mathematical and probabilistic predictions, (2) is explicit, transparent, and readily available for review or reassessment, and (3) accounts for uncertainty in predictions and assumptions and allows that uncertainty to be incorporated into the decision making framework. This type of framework removes the subjectivity that is often present when making management decisions related to take requests for research or conservation purposes and ultimately helps screen policies and management actions to find the best choices to deliver intended conservation benefits.

Population viability analysis (PVA) models are very common in assessing the risk of extinction for many plant and animal populations (Reed et al. 1998, 2002), but these models are not without criticism (Coulson et al. 2001; Ellner et al. 2002). A common criticism of PVA models is that their ability to accurately assess extinction rates is low because available data for most threatened

TABLE 3. Minimum numbers of female Humpback Chub by size to be translocated annually for the first 5 years only of a 50-year simulation from the Little Colorado River (donor) to a small, medium, and large stream (recipients) before extinction probability is <10% for 1,000 trials. Low and high carrying capacity (as number of age-1 and older females) for each stream was estimated as follows: Little Colorado River = 4,000–9,000; small stream = 104–156; medium stream = 291–437; large stream = 2,000–2,500. Each run is 1,000 simulations for 50 years and a compensation ratio *CR* of 2 (low) or 4 (high). The number of female fish stocked, the extinction probability (%), and the estimated number of subadult (age 1 to age 3) and adult (age 4 and older) are presented.

		Number female fish stocked (extinction probability) (Estimated final mean number of subadult and adult fish after 50 years)		
Size (mm)	Compensation ratio	Small stream	Medium stream	Large stream
<30	Low	1,200 (∼8%) (subadults: 61) (adults: 21)	1,300 (∼9%) (subadults: 38) (adults: 14)	1,000 (∼9%) (subadults:74) (adults: 25)
	High	1,100 (∼9%) (subadults: 62) (adults: 21)	1,200 (∼9%) (subadults: 46) (adults: 17)	1,100 (∼9%) (subadults: 82) (adults: 27)
30–60	Low	125 (∼9%) (subadults:58) (adults: 21)	125 (∼9%) (subadults: 39) (adults: 14)	125 (∼9%) (subadults: 79) (adults: 26)
	High	115 (9%) (subadults:60) (adults: 21)	125 (∼9%) (subadults:46) (adults: 17)	125 (∼8%) (subadults: 82) (adults: 27)
60–80	Low	30 (∼9%) (subadults:57) (adults: 20)	30 (∼9%) (subadults: 39) (adults: 15)	30 (∼9%) (subadults: 81) (adults: 27)
	High	30 (∼8%) (subadults:66) (adults: 23)	30 (∼9%) (subadults: 47) (adults: 17)	30 (∼9%) (subadults: 84) (adults: 27)
80–130	Low	15 (∼9%) (subadults:62) (adults: 22)	15 (∼8%) (subadults: 40) (adults: 15)	15 (∼8%) (subadults: 82) (adults: 27)
	High	15 (∼7%) (subadults:67) (adults: 23)	15 (∼7%) (subadults: 47) (adults: 17)	15 (∼8%) (subadults: 89) (adults: 29)

species is limited (Ellner et al. 2002). Humpback Chub have been studied extensively for 20+ years and many key population parameters are directly estimable for this population (Table 1). Our model directly incorporates uncertainty in many of these population parameters such as variation in survival, which follows recommendations from Coulson et al. (2001) and others that PVA model input parameters capture the distribution of possible values. We also present our results in terms of population trajectories based on 1,000s of PVA model simulations, each an individual population trajectory based on 100s or 1,000s of individual fish (the IBM) using a set of parameter-starting values drawn from Table 1. Individual-based models are very widely used in ecology and by design capture variation among individual animals (i.e., growth, fecundity) and the environments they encounter (i.e., mortality rates) (DeAngelis and Mooij 2005). By presenting the distribution of large numbers of individual population trajectories, based on IBM simulations from a large number of individual animals (Figures 1–3), managers are able to easily assess the full range of possible outcomes in terms of extinction risk (Scenarios 1 and 2) or population establishment (Scenario 3).

Like all models, our model relied on a variety of key parameters and assumptions that we calculated for Humpback Chub, borrowed from similar species, or estimated based on our collective knowledge. We found that even with a compensation ratio lower (and thus more conservative) than any measured value for fish populations (Myers et al. 1999; Goodwin et al. 2006; Ricard et al. 2012), the Little Colorado River population of Humpback Chub is (1) resilient to catastrophic mortality events (Scenario 1) and (2) unlikely to be put at any higher risk of extinction under any of the permitted take requests recently proposed for research purposes (e.g., <100 larvae or small juveniles for otolith collection) or for translocation or refuge development purposes (600–800 individuals between 30 and 80 mm TL; Scenarios 2). Additionally we found that under translocation scenarios evaluated to three candidate streams, there are large differences in the numbers of fish required for low extinction probability (<10%) dependent on fish size (Scenario 3).

A key assumption in our model and associated policy recommendations is the role of the compensation ratio *CR* in our population predictions. The *CR* describes the relative improvement in juvenile survival at low stock abundance compared to the stock at natural size. This ratio represents the recruitment compensation potential of the population (Goodyear 1980). Higher *CR* values imply populations that have higher compensatory juvenile survival at low population sizes relative to unexploited population sizes. This implies that high *CR* populations are more resilient than populations with low *CR* values because they have a stronger compensatory response (Walters and Martell 2004). Populations with higher *CR* values would thus recover from catastrophe (Scenario 1), be resilient to permitted take (Scenario 2), or expand to carrying capacity quickly when translocated to other streams (Scenario 3). Our use of very conservative *CR* values of 2 and 4 in our modeling scenarios follows recommendations from McGowan and Ryan (2010) of considering the role of compensation in assessing the potential impacts of removals on an endangered species.

Because of high fecundity in most fish populations, the potential to produce large numbers of eggs and potentially large numbers of small juveniles exists even when populations are low. Our simulations used the only published estimates of fecundity for Humpback Chub (Hamman 1982a) of about 2,500 eggs per female. These estimates were based on induced ovulation and manual stripping of female Humpback Chub in a hatchery setting. There is some evidence to suggest that Humpback Chub or similar species use a batch spawning strategy (Johnston and Page 1992) such that the annual fecundity estimates are likely much higher than those reported by Hamman (1982a). For example, estimates for the congeneric Bonytail averaged about 25,000 eggs/fish for slightly larger fish (487–564 mm TL; Hamman 1982b) and Roundtail Chub averaged about 18,700 eggs/fish for mostly smaller fish (Brouder et al. 2006) than the Humpback Chub (355–406 mm) assessed by Hamman (1982a). The length differences alone did not fully account for the intraspecific (and likely the interspecific) differences in eggs per female reported. As such, using the published estimates of Hamman (1982a) for Humpback Chub makes our results assessing impacts to the donor population conservative.

Beverton and Holt (1957) examined the relation between parental spawning stock and subsequent recruitment and mortality rates of juvenile fish. These authors noticed that the relationship between spawning stock (number of adults) was generally a poor predictor of recruitment except at low parental stock sizes and they suggested that this was because juvenile mortality rates must decline when fewer eggs are produced. If juvenile mortality rates were not strongly density dependent, then recruitment would increase across a range of stock size, which is not what data from more than 300 different fish stocks show (Myers et al. 1999; Goodwin et al. 2006; Ricard et al. 2012). In our model, this compensatory improvement is partitioned into each of the life stages specified along the Beverton–Holt curve. Compensation in survival is likely related to the ability of juvenile organisms to select habitat that reduced competitive interactions at small spatial and temporal scales. The diversity of these "foraging-arenas" (Ahrens et al. 2012) available in natal habitats is likely to determine the strength of compensation when abundance declines. At lower juvenile densities, remaining individuals, such as Humpback Chub translocated to a recipient stream, have more food resources available, spend less time searching for food, and as a result have reduced exposure to predation. All of these factors may combine to lead to higher survival at lower stock sizes and lower risk of extinction, which influences the rate of establishment in translocated populations.

One interesting aspect of our results is informing the size and number of Humpback Chub to be translocated to the different tributary populations. In comparing number of individuals available to be cropped from the Little Colorado River population, from the largest female juveniles (80–130 mm TL) to larvae (<30 mm TL) we found that stocking densities were nearly 30× different (Table 2). The extinction risk to the Little Colorado River population from removals of larvae or juveniles at the levels calculated in Scenario 3 is negligible. As an example, Table 2 demonstrates that removal of 10% of female larvae from the Little Colorado River yields at least 25,000–26,000 larvae per year over the 5-year removal period. Results from Scenario 3 in Table 3 however suggest that only about 1,000–1,300 female larvae need to be stocked per year for a 5-year period to establish a population with an extinction probability of <10% in each tributary (assuming similar growth and survival rates as the Little Colorado River and zero emigration from recipient stream, see below). From a practical perspective it is impossible to determine the sex on larval or juvenile Humpback Chub so in application twice the number of larvae listed in Table 3 would need to be removed. Even at these higher removal levels, the results in Table 2 suggest that the extinction risk to the Little Colorado River donor population would be negligible. This demonstrates that the recommended stocking level is likely only about 1% of the female larvae produced each year in the Little Colorado River and removals of this level are very unlikely to increase extinction risk or lead to any change in the age-1 and older population size (Table 2).

Our results also suggest that managers should be patient in their expectations for translocated Humpback Chub populations to reach carrying capacity. We found that if stocking occurs for 5 years and then the population is monitored for an additional 45 years (total of 50 years), then the expected number of age-1 individuals in the population will still be low, <100 at all stocking sizes and levels. This is not unexpected when compared to Scenario 1 results (Figure 1) that indicate it would take more than 100 years for populations to recover to carrying capacity ($CR = 2$) following our simulated catastrophic mortality event.

One reason for this long period of time required to reach carrying capacity is that the population age structure in the

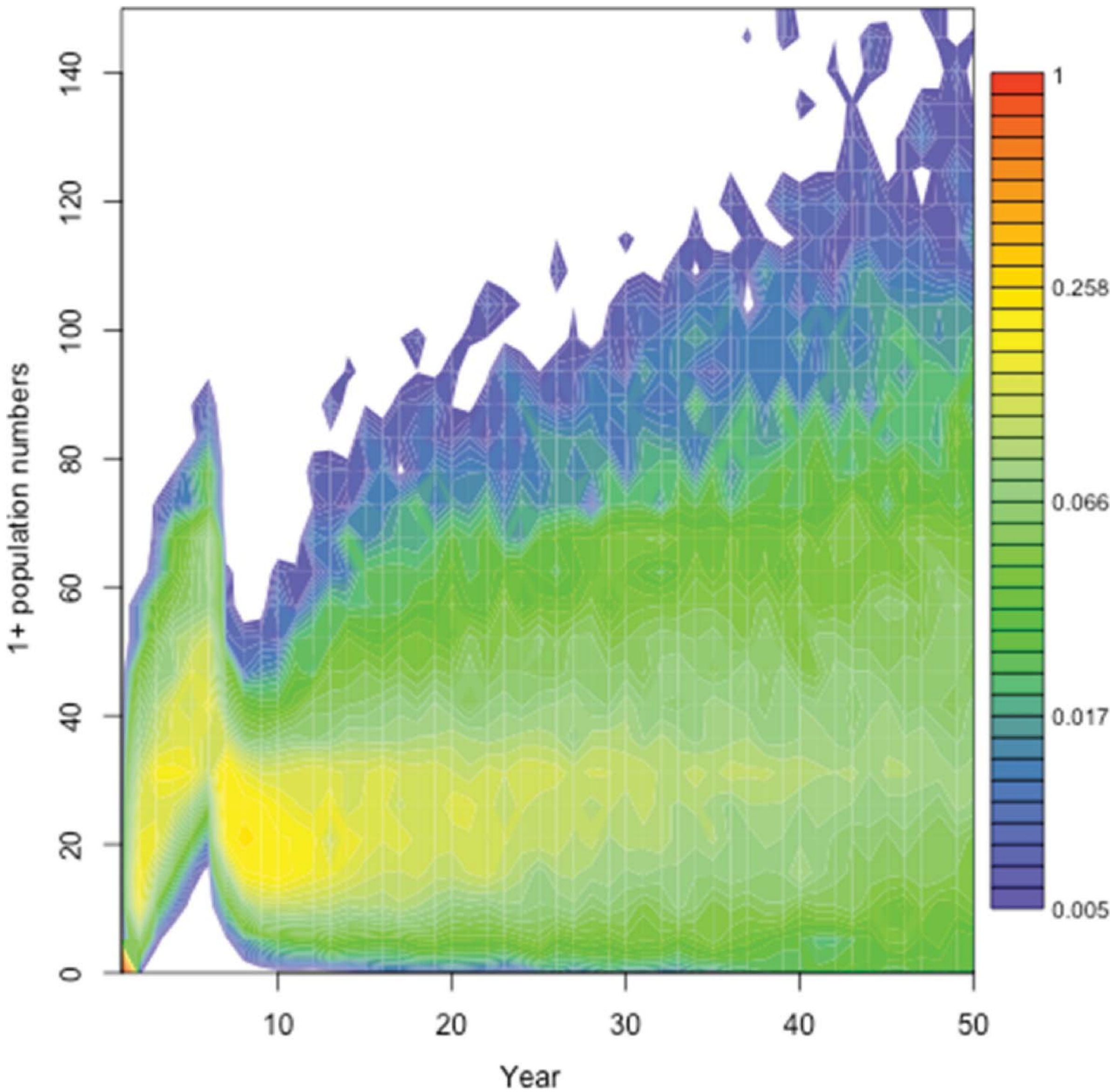

FIGURE 3. Translocation scenario where 30 medium (60–80 mm TL) and 30 large (80–130 mm TL) juveniles are stocked into a recipient stream for a 5-year period, and then the stockings are stopped and the population monitored. Note the rapid build-up in population abundance during the 5-year stocking period, a decline in abundance as the population transitions to becoming self-sustaining, and then a slow build-up in population size. Red colors indicate higher observation densities and dark blue colors indiciate lower observation densities (indicated in the legend) from the 1,000 replicate simulation trials.

recipient stream has to mature into a reproducing, self-sustaining population. As an example, a manager might choose to translocate and stock 30 each of two sizes of juveniles (60–80 mm TL and 80–130 mm TL) for 5 years, in an attempt to accelerate establishment of a population in a tributary system. This initial stocking would lead to a rapid build-up in population size for the first 5 years as the translocated fish were released (Figure 3), but natural mortality would slowly remove these translocated fish leading to declines in the population. At the same time the "survivors" from the initial stocking would continue to grow to reach sexual maturity and their progeny would contribute to the population growth towards carrying capacity. For this newly founded population to be self-sustaining, enough individuals need to survive and spawn to counteract the effects of genetic drift and inbreeding. In general, current conservation guidelines suggest an effective population size (N_e; the number of breeding individuals contributing genetic diversity to future generations) should be a minimum of $N_e = 50$ to prevent genetic drift and inbreeding and an $N_e = 500$ is needed to allow the population to adapt to changing environmental conditions and retain its evolutionary potential (Franklin 1980; Soulé 1987). Ultimately if the translocated population is not able to recruit to adulthood and reproduce then the recipient streams simply become sink populations only maintained by translocations from the Little Colorado River.

Management Implications

Using a PVA model that explicitly accounts for compensation in survival at different life stages, we demonstrated that the Little Colorado River aggregation of Humpback Chub is robust to removals of up to 50% of the larvae or small juveniles over a 5-year period for translocation or research purposes. At these removal levels, the risk of extinction did not increase and generally within 5 years the population had returned to preremoval levels. We found that removals of the the smallest, youngest size-classes (larvae and small juveniles) had the least potential impact on the population of age-1 and older individuals, which is not surprising given that the highest rates of natural mortality are in the earliest life stages. As such, the removal of even 1000s of individuals at these early life stages had basically no predicted impact on the age-1 and older population. We also found that the stocking levels required to have a relatively high probability of establishing additional spawning aggregations in other recipient tributaries was much lower than the removal levels that would put the Little Colorado River donor population at risk of impairment.

These results are of interest to resource managers at several levels. First, incidental take assessments for listed species are often challenging to assess because of an absence of a framework to evaluate the risks to the species from the allowed take (McGowan and Ryan 2010). Our results suggest that for Humpback Chub, and likely other similar species, the risks to these populations from permitted removals of larvae and small juveniles in the numbers required for translocations or for research purposes, such as otolith analyses, are very small. Second, we identified the trade-offs in terms of fish size and number to be translocated from the donor Little Colorado River population to other tributary systems in an attempt to establish additional spawning populations. These guidelines should help to design future translocation efforts, increasing the likelihood of success and reducing costs. We found that the success of translocations is likely dependent on the survival and growth rates of fish in recipient streams being similar to the donor Little Colorado River, and that emigration from the recipient stream is low. Ongoing research led by National Park Service fisheries staff as part of pilot translocation studies have documented that prey resources, flows, temperature, and substrate at least in Shinumo and Havasu creeks are likely suitable to support translocated Humpback Chub populations (B. Healy, unpublished). A key concern however is the presence of nonnative Rainbow Trout (Shinumo, Bright Angel, and Havasu creeks) and Brown Trout (Bright Angel Creek). Removal efforts for Rainbow Trout are ongoing in Shinumo and Havasu creeks to reduce predation risk for translocated Humpback Chub and their progeny. An additional concern is the potentially high rate of emigration from the donor stream by translocated fish because of strong natal homing found in many fish stocks (Dittman and Quinn 1996; Thorrold et al. 2001) even at very small spatial scales (Stewart et al. 2003). The imprinting process is not understood in Humpback Chub (or many other species) and this likely complex process may occur at very early ages such that translocated fish at an early age may be more likely to have already imprinted on the donor stream before reaching the recipient stream. Additionally, some emigration may occur rapidly following the initial release of translocated individuals (e.g., Shinumo Creek; Spurgeon 2012) and acclimation of translocated individuals to the recipient stream may reduce the emigration response or potentially predator encounters (Brennan et al. 2006). As an example, if we translocated 30 60–80-mm-TL juveniles and thirty 80–130-mm-TL juveniles into the stream with a small carrying capacity of 300 individuals for 5 years, we can expect at the end of 50 years to have about 120 age-1 and older Humpback Chub in this stream at an extinction risk of $<1\%$. However, if we suspect that about 40% of the age-1 fish will either emigrate or die at a higher rate than the Little Colorado River (perhaps from a novel nonnative predator), then we can expect that at the end of that 50-year time period only 25 age-1 and older Humpback Chub to be present. If all translocated fish are susceptible to some sort of mass emigration or mortality event due to the donor stream being unsuitable, then the extinction risk in the donor stream will be very high. This highlights the clear need to carefully assess the recipient stream for risks to the translocation success from factors such as nonnative predators and also to think about the biology of the fish being translocated from their donor stream, especially as it relates to factors with as strong an evolutionary significance as natal imprinting.

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REFERENCES

Ahrens, R. N. M., C. J. Walters, and V. Christensen. 2012. Foraging arena theory. Fish and Fisheries 13:41–59.

Andersen, M. E., M. W. Ackerman, K. D. Hilwig, A. E. Fuller, and P. D. Alley. 2010. Evidence of young Humpback Chub overwintering in the mainstem Colorado River, Marble Canyon, Arizona, USA. Open Fish Science Journal 3:42–50.

BCME (British Columbia Ministry of Environment). 2006. Incident summary report, CN Rail: August 5, 2005 spill of 40,000 litres of 73% solution of sodium hydroxide into the Cheakamus River north of Squamish British Columbia. BCME, Environmental Protection, Lower Mainland Region, DGI 561257, Surrey. Available: www.env.gov.bc.ca/epd/regions/lower_mainland/special_studies/cheakamus/cheakamus.pdf. (January 2013).

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Springer-Science, Dordrecht, The Netherlands.

Brennan, N. P., M. C. Darcy, and K. M. Leber. 2006. Predator-free enclosures improve post-release survival of stocked Common Snook. Journal of Experimental Marine Biology and Ecology 335:302–311.

Brouder, M. J., D. D. Rogers, and L. D. Avenetti. 2006. Observations on the reproductive biology of Roundtail Chub, *Gila robusta,* in the upper Verde River, Arizona. Western North American Naturalist 66:260–262.

Clarkson, R. W., and M. R. Childs. 2000. Temperature effects on hypolimnial-release dams on early life stages of Colorado River basin big-river fishes. Copeia 2000:402–412.

Coggins, L. G., Jr., W. E. Pine III, C. J. Walters, and S. J. D. Martell. 2006. Age-structured mark–recapture analysis: a virtual-population-analysis-based model for analyzing age-structured capture–recapture data. North American Journal of Fisheries Management 26:201–205.

Coggins, L. G., Jr., and C. J. Walters. 2009. Abundance trends and status of the Little Colorado River population of Humpback Chub: an update considering data from 1989–2008. U.S. Geological Survey, Open-File Report 2009–1075, Reston, Virginia.

Coggins, L. G., Jr., M. D. Yard, and W. E. Pine III. 2011. Nonnative fish control in the Colorado River in Grand Canyon, Arizona: an effective program or serendipitous timing? Transactions of the American Fisheries Society 140:456–470.

Converse, Y. K., C. P. Hawkins, and R. A. Valdez. 1998. Habitat relationships of subadult Humpback Chub in the Colorado River through Grand Canyon: spatial variability and implications of flow regulation. Regulated Rivers: Research and Management 14:267–284.

Coulson, T., G. M. Mace, E. Hudson, and H. Possingham. 2001. The use and abuse of population viability analysis. Trends in Ecology and Evolution 16:219–221.

DeAngelis, D. L., and W. M. Mooij. 2005. Individual-based modeling of ecological and evolutionary processes. Annual Review of Ecology, Evolution, and Systematics 36:147–168.

DeAngelis, D. L., and K. A. Rose. 1992. Which individual-based approach is most appropriate for a given problem? Pages 67–87 *in* D. L. DeAngelis and L. J. Gross, editors. Individual-based models and approaches in ecology: populations, communities, and ecosystems. Chapman and Hall, New York.

Dittman, A. H., and T. P. Quinn. 1996. Homing in Pacific salmon: mechanisms and ecological basis. Journal of Experimental Biology 199:83–91.

Ellner, S. P., J. Fieberg, D. Ludwig, and C. Wilcox. 2002. Precision of population viability analysis. Conservation Biology 16:258–261.

Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135–150 *in* M. E. Soulé and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, Massachusetts.

Goodwin, N. B., A. Grant, A. L. Perry, N. K. Dulvy, and J. D. Reynolds. 2006. Life history correlates of density-dependent recruitment in marine fishes. Canadian Journal of Fisheries and Aquatic Sciences 63: 494–509.

Goodyear, C. P. 1980. Compensation in fish populations. Pages 253–280 *in* C. H. Hocutt and J. R. Stauffer, editors. Biological monitoring of fish. DC Heath and Company, Lexington, Massachusetts.

Gorman, O. T., and D. M. Stone. 1999. Ecology of spawning Humpback Chub, *Gila cypha,* in the Little Colorado River near Grand Canyon, Arizona. Environmental Biology of Fishes 55:115–133.

Hamman, R. L. 1982a. Spawning and culture of Humpback Chub. Progressive Fish-Culturist 44:213–216.

Hamman, R. L. 1982b. Induced spawning and culture of Bonytail Chub. Progressive Fish-Culturist 44:201–203.

Hilborn, R., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, New Jersey.

Hunt, T. A., D. L. Ward, C. R. Propper, and A. C. Gibb. 2012. Effects of capture by trammel net on Colorado River native fishes. Journal of Fish and Wildlife Management 3:133–141.

Johnston, C. E., and L. M. Page. 1992. The evolution of complex reproductive strategies in North American minnows (Cyprinidae). Pages 600–621 *in* R. L. Mayden, editor. Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford, California.

Kaeding, L. R., and M. A. Zimmerman. 1983. Life history and ecology of the Humpback Chub in the Little Colorado and Colorado rivers of the Grand Canyon. Transactions of the American Fisheries Society 112:577–594.

Letcher, B. H., J. A. Priddy, J. R. Walters, and L. B. Crowder. 1998. An individual-based, spatially explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. Biological Conservation 86:1–14.

Lorenzen, K. 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. Canadian Journal of Fisheries and Aquatic Sciences 57:2374–2381.

McGowan, C. P., and M. R. Ryan. 2009. A quantitative framework to evaluate incidental take and endangered species population viability. Biological Conservation 142:3128–3136.

McGowan, C. P., and M. R. Ryan. 2010. Arguments for using population models in incidental take assessments for endangered species. Journal of Fish and Wildlife Management 1:183–188.

Meretsky, V. J., R. A. Valdez, M. E. Douglas, M. J. Brouder, O. T. Gorman, and P. C. Marsh. 2000. Spatiotemporal variation in length–weight relationships of endangered Humpback Chub: implications for conservation and management. Transactions of the American Fisheries Society 129: 419–428.

Moussalli, E., and R. Hilborn. 1986. Optimal stock size and harvest rate in multistage life history models. Canadian Journal of Fisheries and Aquatic Sciences 43:135–141.

Myers, R. A., K. G. Bowen, and N. J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56:2404–2419.

NRC (National Research Council). 1995. Science and the endangered species act. National Academy Press, Washington, D.C.

Oberlin, G. E., J. P. Shannon, and D. W. Blinn. 1999. Watershed influence on the macroinvertebrate fauna of ten major tributaries of the Colorado River through Grand Canyon, Arizona. Southwestern Naturalist 44:17–30.

Omana-Smith, E. C., B. D. Healy, W. C. Leibfried, and D. P. Whiting. 2012. Bright Angel Creek trout reduction project: winter 2010–2011 report. National Park Service, Natural Resource Technical Report NPS/GRCA/NRTR–2012/646, Fort Collins, Colorado. Available: www.nature.nps.gov/publications/nrpm/nrtr.cfm#2012. (February 2013).

Paukert, C. P., L. G. Coggins Jr., and C. E. Flaccus. 2006. Distribution and movement of Humpback Chub in the Colorado River, Grand Canyon, based on recaptures. Transactions of the American Fisheries Society 135:539–544.

Pulwarty, R. S., and T. S. Melis. 2001. Climate extremes and adaptive management on the Colorado River: lessons from the 1997–1998 ENSO event. Journal of Environmental Management 63:307–324.

Reed, J. M., L. S. Mills, J. B. Dunning Jr., E. S. Menges, K. S. McKelvey, R. Frye, S. R. Beissinger, M. C. Anstett, and P. Miller. 2002. Emerging issues in population viability analysis. Conservation Biology 16:7–19.

Reed, J. M., D. Murphy, and P. F. Brussard. 1998. The efficacy of population viability analysis. Wildlife Society Bulletin 26:244–251.

Ricard, D., C. Minto, O. P. Jensen, and J. K. Baum. 2012. Examining the knowledge base and status of commercially exploited marine species with the RAM legacy stock assessment database. Fish and Fisheries 13: 380–398.

Ryel, R. J., and R. A. Valdez. 1995. Development of a population model for Humpback Chub (*Gila cypha*) in Grand Canyon: supplement 5—life history and ecology of the Humpback Chub (*Gila cypha*) in the Colorado River, Grand Canyon, Arizona. U.S. Bureau of Reclamation, Upper Colorado River Region, Salt Lake City, Utah.

Soulé, M. E. 1987. Introduction. Pages 1–10 *in* M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, UK.

Stewart, I. J., T. P. Quinn, and P. Bentzen. 2003. Evidence for fine-scale natal homing among island beach spawning Sockeye Salmon, *Oncorhynchus nerka*. Environmental Biology of Fishes 67:77–85.

Stone, D. M. 2010. Overriding effects of species-specific turbidity thresholds on hoop-net catch rates of native fishes in the Little Colorado River, Arizona. Transactions of the American Fisheries Society 139:1150–1170.

Stone, D. M., and O. T. Gorman. 2006. Ontogenesis of endangered Humpback Chub (*Gila cypha*) in the Little Colorado River, Arizona. American Midland Naturalist 155:123–135.

Thorrold, S. R., C. Latkoczy, P. K. Swart, and C. M. Jones. 2001. Natal homing in a marine fish metapopulation. Science 291:297–299.

Trammell, M., B. Healy, E. Omana Smith, and P. Sponholtz. 2012. Humpback Chub translocation to Havasu Creek, Grand Canyon National Park: implementation and monitoring plan. National Park Service, Natural Resource Report NPS/GRCA/NRR – 2012/586, Fort Collins, Colorado. Available: www.nature.nps.gov/publications/nrpm/nrr.cfm#2012. (February 2013).

USBOR (U.S. Bureau of Reclamation). 1995. Operation of Glen Canyon Dam: final environmental impact statement. USBOR, Upper Colorado River Region, Salt Lake City, Utah.

USFWS (U.S. Fish and Wildlife Service). 2008. Final biological opinion for the operation of Glen Canyon Dam (February 27, 2008). USFWS, Arizona Ecological Services, Phoenix.

USFWS (U.S. Fish and Wildlife Service). 2010. A genetic management plan for captive and translocated endangered Humpback Chub in the lower Colorado River basin. USFWS, Dexter National Fish Hatchery and Technology Center, Dexter, New Mexico.

USFWS (U.S. Fish and Wildlife Service). 2011. Final biological opinion on the operation of Glen Canyon Dam including high flow experiments and nonnative fish control (December 23, 2011). USFWS, Arizona Ecological Services, Phoenix. Available: www.fws.gov/southwest/es/arizona/Documents/Biol_Opin/110112_HFE_NNR.pdf. (January 2013).

Valdez, R. A., S. W. Carothers, M. E. Douglas, M. Douglas, R. J. Ryel, K. R. Bestgen, and D. L. Wegner. 2000. Research and implementation plan for establishing a second population of Humpback Chub in Grand Canyon. U.S. Department of the Interior, Grand Canyon Monitoring and Research Center, Final Report, Flagstaff, Arizona.

Valdez, R. A., and W. J. Masslich. 1999. Evidence of reproduction by Humpback Chub in a warm spring of the Colorado River in Grand Canyon, Arizona. Southwestern Naturalist 44:384–387.

Van Haverbeke, D. R., D. M. Stone, and M. J. Pillow. 2011. Mark–recapture and fish monitoring activities in the Little Colorado River in Grand Canyon during 2010. Annual Report to U.S. Geological Survey, Grand Canyon Monitoring and Research Center, Flagstaff, Arizona.

Walters, C. J., and S. J. D. Martell. 2004. Fisheries ecology and management. Princeton University Press, Princeton, New Jersey.

Webb, R. H., T. S. Melis, and R. A. Valdez. 2002. Observations of environmental change in Grand Canyon, Arizona. U.S. Geological Survey, Water-Resources Investigations Report 02-4080, Tucson, Arizona.

Yard, M. D., L. G. Coggins Jr., C. V. Baxter, G. E. Bennett, and J. Korman. 2011. Trout piscivory in the Colorado River, Grand Canyon: effects of turbidity, temperature, and fish prey availability. Transactions of the American Fisheries Society 140:471–486.