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ARTICLE

Establishment of a Reproducing Population of Endangered Humpback Chub through Translocations to a Colorado River Tributary in Grand Canyon, Arizona

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Abstract
Translocations, defined herein as the human-assisted movement of individuals from a source population to other waters within their historical range, are prevalent in recovery plans for endangered fishes. Many translocations fail to establish new populations, however, and outcomes are often poorly documented. Endangered Humpback Chub *Gila cypha* persist as a self-sustaining population in Grand Canyon, Arizona, despite threats from introduced nonnative competitors and predators and modified flow, thermal, and sediment regimes due to river regulation. In the decades following the completion of Glen Canyon Dam, the Grand Canyon population has been primarily sustained through reproduction in a single Colorado River tributary, the Little Colorado River (LCR). To establish population redundancy and aid in recovery, we annually translocated between 243 and 509 juvenile Humpback Chub from the LCR to Havasu Creek, a smaller Colorado River tributary in Grand Canyon National Park. Juvenile Humpback Chub were collected from the wild and reared in a hatchery for 8–12 months prior to the translocations. Through biannual mark–recapture sampling in Havasu Creek, we estimated annual abundance for all of the translocated cohorts and found

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that apparent survival and growth rates met or exceeded the demographic rates that are published for the LCR. We observed reproductively mature adults each year in May, beginning in 2012, and untagged juvenile Humpback Chub beginning in the following year and every year thereafter, with results that indicated successful reproduction. Beginning in 2016, we noted recruitment to maturity of fish that were produced in situ and the population's abundance increased through 2018, indicating potential for the establishment of a self-sustaining population. As an example of the successful translocation of an endangered species that demonstrates the potential importance of tributaries in the recovery of large-river fishes, our study may help to inform future recovery planning.

At least 39% of North American freshwater fishes were imperiled as of 2008 (Jelks et al. 2008), and extinction rates are expected to increase (Burkhead 2012). This alarming projected loss of freshwater biota continues to accelerate due to persistent and emerging threats including habitat degradation, species invasions, and climate change (reviewed in Reid et al. 2019). To counteract these losses, proactive conservation measures that are intended to lead to the establishment of new populations are common in recovery plans for endangered fishes but in many cases the outcomes are not properly documented or reintroduction or translocation attempts fail (Minckley 1995; George et al. 2009; Vincenzi et al. 2012). For example, in a review of 10 translocations of endangered Bull Trout *Salvelinus confluentus*, seven had unknown outcomes (Hayes and Banish 2017).

Translocations, defined herein as the human-assisted movement of individuals from a source population to other waters within their historical range, are a potential mechanism through which to accomplish recovery goals. Natural dispersal is simulated, and enhanced population resiliency and redundancy can be achieved through translocations where suitable habitat is excessively fragmented (Minckley 1995). Rearing opportunities may also be enhanced through translocations of juveniles to suitable nursery habitats, leading to population security where juvenile survival and recruitment is identified as a limiting factor (Trammell et al. 2012; Spurgeon et al. 2015b). Given the prevalence of reintroductions and translocations in recovery plans, there is a clear need to evaluate these activities quantitatively to determine their efficacy in recovering endangered or threatened species and informing future efforts (Minckley 1995; Sheller et al. 2006; George et al. 2009; Olden et al. 2011; Cochran-Biederman et al. 2015).

Fishes of the southwestern region of the United States, where arid-land aquatic habitats are remarkably vulnerable to intensive and expanding human freshwater use, are particularly imperiled (Sabo et al. 2010; Budy et al. 2015; Ruhí et al. 2016). Declining streamflow, which is exacerbated by the ongoing and projected effects of climate change (McHugh et al. 2008; Dettinger et al. 2015; Ruhí et al. 2016), dam construction and fragmentation (Fagan et al. 2002; Kominoski et al. 2018), and negative biological interactions with invasive fishes (Olden et al. 2006) all threaten the persistence of highly endemic fauna, including those of the Colorado River (Holden and Stalnaker 1975). Dam and reservoir constructions throughout the Colorado River basin have facilitated the proliferation of lentic nonnative fishes that have been introduced for sport fishing by stabilizing the historical disturbance regime that is characteristic of the rivers that flow through arid lands (Olden et al. 2006; Mims and Olden 2012). These combined influences have led to declines in the distribution and abundance of several of the Colorado River basin's unique endemic fishes, resulting in their being listed under the U.S. Endangered Species Act.

In the Grand Canyon segment of the Colorado River, juvenile native fishes, including those of endangered Humpback Chub *Gila cypha*, have suffered from low recruitment due to cold hypolimnetic water that has been released by the Glen Canyon Dam since 1963 (Robinson and Childs 2001; Petersen and Paukert 2005; Pine et al. 2017). Inhibited growth, delayed maturity, and prolonged vulnerability to predation by nonnative salmonids limit the survival of juveniles in the Colorado River tailwater (Yackulic et al. 2014; Ward and Morton-Starner 2015; Ward et al. 2016). This important population, which is the largest remaining in the entire basin (USFWS 2018b), has been sustained primarily by reproduction in a single tributary, the Little Colorado River (LCR; Valdez and Masslich 1999; Valdez et al. 2000). The vulnerability of this sole spawning area prompted managers to explore means by which to establish population redundancy in Grand Canyon and improve juvenile rearing and recruitment to maturity (Valdez et al. 2000; Trammell et al. 2012; USDOI 2016). Other Grand Canyon tributaries may support fewer exotic predators and competitors, and they may exhibit less flow or thermal alteration than that which occurs in the Colorado River, providing good opportunities to test the efficacy of translocations to establish redundancy in the Humpback Chub population (Valdez et al. 2000). However, these smaller tributaries, some of which are isolated from the Colorado River by barriers to fish movement, may not support large populations of Humpback Chub, potentially leading to a low probability of establishment (Pine et al. 2013). These isolated refuges may contain habitat that is only marginally suitable to support all life stages, or carrying capacity may be insufficient to maintain genetically diverse and sustainable populations, resulting in failed efforts to restore or maintain isolated populations (Fausch et al. 2009).

Translocations of Humpback Chub have been applied within the LCR itself (Van Haverbeke et al. 2013) and from the LCR to another smaller tributary, Shinumo Creek, in Grand Canyon (Spurgeon et al. 2015b). Both efforts were successful in promoting the growth and survival of juveniles, but high emigration rates that were associated with flooding (Van Haverbeke et al. 2013; Spurgeon et al. 2015b) or competition with nonnative fishes may have limited the persistence and establishment of new populations (Pine et al. 2013; Spurgeon et al. 2015a). Nevertheless, substantial numbers of Humpback Chub that have dispersed from translocation sites have been observed later integrating with downstream aggregations in the LCR (Van Haverbeke et al. 2013) or in other reaches of the Colorado River (Van Haverbeke et al. 2017; Rogowski et al. 2018), meeting management goals for rearing. For example, one goal for the conservation of Humpback Chub in Grand Canyon is to expand the role of tributaries in increasing the distribution and size of aggregations in the Colorado River (USFWS 2011:12).

Beginning in 2011, we translocated juvenile Humpback Chub from the LCR, to Havasu Creek, a Colorado River tributary. In this paper, we present the results of our analyses of apparent survival, absolute growth, and reproduction and recruitment of cohorts of translocated Humpback Chub in Havasu Creek. We assessed the efficacy of this effort for conservation by measuring these demographic rates against those for juveniles in the LCR, the Colorado River, and Shinumo Creek. Comparable results to those that were found for the donor population, which is assumed to be self-sustaining (USFWS 2018a), would signal the likelihood of the long-term sustainability of a translocated population (Pine et al. 2013).

METHODS

Study area.— Humpback Chub were collected from the LCR prior to their release into Havasu Creek, downstream of the boundary of the Havasupai Indian Reservation within Grand Canyon National Park (GCNP; Figure 1). The study area and existing fish assemblage prior to the translocations are described in detail in Trammell et al. (2012), but we briefly summarize these details below. Translocations and monitoring occurred over 5.6 km of Havasu Creek within GCNP, bounded on the upstream end by a presently impassable waterfall that is located near the boundary between the Havasupai Indian Reservation and GCNP and on the lower end by a series of cascades that are approximately 100 m upstream of the mouth. The cascades appear to impede upstream fish passage from the Colorado River for most fishes, as many Flannelmouth Suckers *Catostomus latipinnis* congregate in

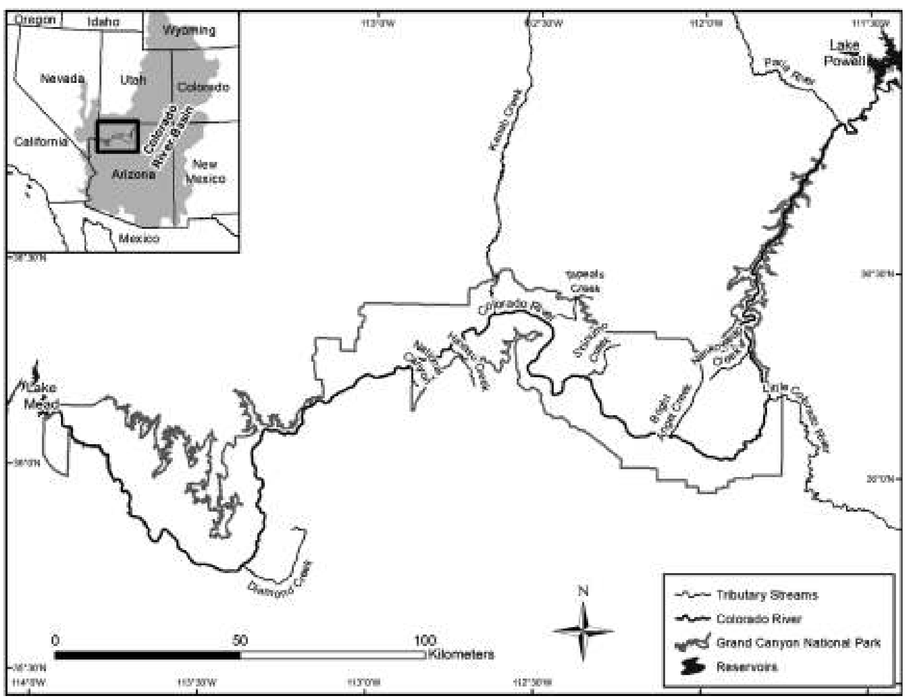

FIGURE 1. Map of the study area, including the location of Havasu Creek (center of map) and the Little Colorado River (right side of map), within Grand Canyon National Park, Arizona. The Colorado River basin delineation is shaded in the inset.

the mouth below the cascades during spawning periods but are not captured above (Appendix Table A.1; B. D. Healy, personal observation). During rare periods of sustained high Colorado River flows, such as those that occur during the Glen Canyon Dam discharges that are meant to transfer water to Lake Mead beginning in spring of 2011 ("equalization flows"), these lower cascades may be inundated and allow for fish passage (Trammell et al. 2012). While equalization flows can occur more frequently, those of 2011 were unique in that dam discharge remained greater than 622 m^3/s and it was relatively steady from early May through the end of August, 2011 (U.S. Geological Survey [USGS] data, gauge 09383100). Cascades throughout the creek are developed from the calcium carbonate precipitation and cementation that form travertine dams.

In a feasibility study of the establishment of a second spawning population in Grand Canyon, Valdez et al. (2000) identified Havasu Creek—the tributary that is most similar to the LCR in water chemistry and habitat (Table 1)—as the location that is most likely to support Humpback Chub. Despite its similar water chemistry, the base flow in Havasu Creek is only 26% of that in the LCR (1.8 m^3/s versus 7 m^3/s, Valdez et al. 2000). However, its reliable spring-fed flow regime is relatively unmodified, with no large impoundments and few irrigation diversions, which are located mainly in the small community of Supai Village, Arizona, upstream of the study area (Melis et al. 1996). Large, short-lived monsoonal floods that exceed 20 m^3/s occur in Havasu Creek on an annual basis, and the floods occasionally exceed 300 m^3/s, primarily during the summer months (USGS data, gauge 09404115). On rare occasions over the past century, large damaging floods (~575 m^3/s) occurred that uprooted large trees, altered travertine deposits, and transported large volumes of materials to the Colorado River (Melis et al. 1996).

The general temperature thresholds for the successful growth and reproduction of Humpback Chub were found to be 12°C and 16°C, respectively (Hamman 1982). Havasu Creek is much warmer and more thermally suitable for Humpback Chub than the Colorado River in Grand Canyon is, and it is similar to the LCR (Voichick and Wright 2007). Between 2011 and 2018, the water temperatures that are necessary for the reproduction and growth of Humpback Chub were exceeded on 64% and 98% of the days, respectively, in Havasu Creek (USGS data, gauge 09404115) and seasonally the temperature ranges between 9.7°C and 26.2°C (Voichick and Wright 2007). In comparison, water temperatures in the LCR (USGS data, gauge 09402300) and the Colorado River near the mouth of the LCR (USGS data, gauge 09383100) exceeded the thresholds for reproduction and growth 68% and 94% and 0% and 43% of the days, respectively, over the same period.

The fish communities in the LCR and Havasu Creek differed considerably. The fish community in the LCR is dominated by native fishes, but invasive species including Fathead Minnow *Pimephales promelas*, Common Carp *Cyprinus carpio*, several other small-bodied species, Rainbow Trout *Oncorhynchus mykiss*, and Brown Trout *Salmo trutta* also occur (Van Haverbeke et al. 2013). Humpback Chub were not known to be present in Havasu Creek upstream of the lower cascades in the years prior to our study, but surveys were infrequent and not well documented both pre- and postdam (Carothers and Minckley 1981; Valdez et al. 2000; Linder et al. 2012, their 2006 surveys). The reason for the absence of Humpback Chub from Havasu Creek is open to speculation; however, habitat volume (Valdez et al. 2000), or as suggested by Melis et al. (1996), severe floods could limit the abundance of Humpback Chub. Prior to the initial translocations, we conducted two fish community surveys within Havasu Creek, one in February 2010 and another June 2011 (Trammell et al. 2012). We captured native Speckled Dace *Rhinichthys osculus* and Bluehead Sucker *Catostomus discobolus* as well as small numbers of invasive Rainbow Trout during both surveys. Surprisingly, we captured seven adult-sized (>195 mm TL) Humpback Chub during the June survey, which we attributed to the 2011

TABLE 1. Translocation data, including collection date(s), the date of PIT-tagging and release, and size and number of Humpback Chub that were released into Havasu Creek between 2011 and 2016. In 2013, when multiple collections were needed to achieve numeric targets for translocations, the approximate proportion of Humpback Chub that was collected during each excursion is included.

Collection dates (percent of cohort collected)	Hatchery tagging date	Mean length (mm)	Mean weight (g)	Release date	*N*
Nov 5, 2010	May 5, 2011	86.1	4.8	Jun 28, 2011	243
Nov 9, 2011	May 10, 2012	124.7	16.7	May 13, 2012	298
Jul 12, 2012	May 9, 2013	123.1	14.9	May 14, 2013	300
May 24, 2013 (15%), Jul 11, 2013 (20%),	May 9, 2014	123	16.4	May 14, 2014	300
and Nov 7, 2013 (65%)		124	16.4	Jun 5, 2014	209
May 1, 2014	May 13, 2015	131	20.3	May 20, 2015	300
May 28, 2015	May 10, 2016	130	18.5	May 18, 2016	305

equalization flow inundation of the lower cascades, which allowed for upstream passage from the Colorado River. However, we cannot rule out the possibility these fish immigrated to our study reach from other unsurveyed areas of the watershed (i.e., on Havasupai Tribal lands).

Collection, rearing, and translocation.— We collected all of the Humpback Chub from the LCR between 2010 and 2015 at early postlarval (<30 mm TL), juvenile (30–60 mm TL), or subadult (60–135 mm TL) life stages. The timing of our collections varied within a year (spring, summer, and/or fall; Table 1) because it depended on the availability of fish early in the collection year, monsoonal flooding that limited capture, and our effort to target different life stages based on population-viability analyses (Pine et al. 2013). Due to concerns that are related to the potential effect of the translocations on the donor population, we relied on the results of the population-viability analyses to assess the effect of the collections of a range of numbers of fish at different life stages on the abundance and extinction risk to the LCR population (Pine et al. 2013). Until 2014, we targeted juvenile or subadult fish that measured up to 135 mm with baited mini-hoop nets or seines during July or October, as is described in Spurgeon et al. (2015b). We collected postlarval young-of-year fish by using small dip nets in April or May in 2014 and 2015.

Once captured, we held the Humpback Chub temporarily (generally 2–4 d) in net pens in the LCR, transferred them to coolers, and transported them to the canyon rim via helicopter for transfer to a hatchery via truck. The fish were reared for 8–12 months in a hatchery facility that is operated by the state of Arizona, in Cornville, Arizona, (2011 only) or by the U.S. Fish and Wildlife Service (USFWS) in Dexter, New Mexico, to reach a size that was large enough to mark with individual tags. Asian tapeworm *Schyzocytyle acheilognathi* is prevalent in the LCR and infects Humpback Chub (reviewed in Campbell et al. 2019), so newly collected fish were quarantined and treated for common diseases and parasites. The juvenile Humpback Chub were then weighed, measured, and internally tagged with 134.2-kHz, 12.5-mm passive integrated transponder (PIT) tags.

We released the Humpback Chub annually in early summer between 2011 and 2016 (Table 1) in large pools near the upstream extent (2011–2014) or approximately at the midpoint (2015–2016) of the of the study area in Havasu Creek. With the exception of 2014 when we conducted a second translocation in June, we released fish in May in all of the years between 3 and 54 d after tagging them in the hatchery. Tag loss and mortality were expected to be minimal for fish >65 mm TL based on laboratory studies (e.g., Ward et al. 2015) and on our experience with handling translocated Humpback Chub that were released into Shinumo Creek (see Spurgeon et al. 2015b), which is isolated from nontranslocated populations (there are two suspected tag losses out of 417 unique individuals that were recaptured; National Park Service, unpublished data). The tagging procedures that were used in this study were consistent with those that are used in other translocations and laboratory studies. The number and size of the fish that were translocated to Havasu Creek varied among years (Table 1) due to variation in hatchery conditions, the size of the fish that were collected, and disease treatment regimes. On the day of release, the fish were driven to GCNP's South Rim Aviation Center in a hatchery truck, transferred to aerated coolers, and flown to the release site. Upon arrival at the release site, we tempered the water in the coolers with water from Havasu Creek for approximately 1 h, to within 1°C of the temperature in Havasu Creek, to also more closely match other unmeasured water quality parameters. We did not observe any mortality during the transfer, tempering, or release process in any translocation event.

Field sampling.— For the survival analyses, we conducted single-pass posttranslocation trap-netting during each October from 2011 through 2017, with the exception of October 2013 (federal government shutdown) and October 2014 (two-pass netting was conducted). With the exception of 2014, we conducted two-pass netting for abundance estimation during the monitoring trips in May of each year (2012–2018) prior to the release of new cohorts of fish. In this manner, newly translocated fish were included in an annual abundance estimate after 1 year. In May of 2014, two full netting passes were not possible because weather delayed our helicopter support. Spring and fall sampling allowed us to avoid the colder months and turbid summer monsoon conditions that may potentially lower capture efficiency (Stone 2010). We completed each sampling pass over three nights by using two different types of trap nets to target different life stages of native fishes in a variety of slow-water habitats. We set 20 baited mini-hoop nets (50×100 cm, 6-mm nylon mesh, single 10-cm throat) and 40 minnow traps (3.18-mm mesh, $25 \times 25 \times 43$ cm) per night for a total of 60 mini-hoop net and approximately 120 minnow trap sets per pass, baited with Aquamax fish food. We set the nets and minnow traps during the late afternoon and retrieved them early the following day. During spring mark–recapture monitoring, the passes were separated by three nights in a given stream reach to allow the captured fish to mix with the population and to reduce the influence of the behavioral effects of capture (see Trammell et al. 2012). While the fish could theoretically disperse downstream from Havasu Creek between passes, we assumed a closed population due to the 3-d interval between passes.

Our fish handling protocols followed the standardized methodology that was developed by the USGS–Grand Canyon Monitoring and Research Center (Persons et al. 2013). We measured the total length and fork length of all of the fish that were captured to the nearest millimeter, and we weighed all of them to the nearest gram by using a digital scale. All of the Humpback Chub were scanned for a PIT tag, and untagged individuals > 150 mm TL were PIT-tagged. During the two-pass monitoring trips, we marked Humpback Chub < 150 mm TL by clipping the pectoral fin on the first sampling pass. We examined all of the fish for parasites, recorded sex and spawning condition (i.e., expression of gametes and spawning coloration), and live-released all of the native fishes, while euthanizing the nonnative fishes.

Abundance estimation.— We generated annual abundance estimates for each translocated cohort and nontranslocated (those that were produced in situ, or adult immigrants) Humpback Chub for each year between 2012 and 2018. The 2014 abundance estimate was calculated by using the two-pass sampling data from October 2014. To remain consistent with other years' estimates, we excluded the fish that had been translocated during May and June of 2014 from the overall 2014 abundance estimate. The population estimates were generated by using closed-population Huggin's mark–recapture models in Program MARK (White 2008). We considered multiple candidate models, including those with total length covariates for capture probability and group-level identifiers for translocated cohorts and nontranslocated fish, and we used Akaike's information criteria adjusted for small sample sizes (AIC_c) to determine the most parsimonious model (Burnham and Anderson 2002).

Growth.— We calculated cohort-specific seasonal and annual mean daily growth rates (mm/d) by using absolute growth between captures of individual Humpback Chub ($TL_{\text{time-2}} - TL_{\text{time-1}}/\Delta d$) for the first year following the translocations. We summarized the mean growth rates for "winter," defined as the period between October and April, and for "summer," the period between May and September. These two periods encompassed the seasonal thermal differences for Havasu Creek (Voichick and Wright 2007; Trammell et al. 2012), which would influence the growth of juvenile Humpback Chub (Robinson and Childs 2001; Petersen and Paukert 2005), and for the purpose of comparison they are consistent with seasonal growth of juvenile Humpback Chub that was reported by Dzul et al. (2016) for the LCR. We tested for differences in growth rates across cohorts in each season by using analysis of variance (ANOVA), followed by Tukey's honest significant difference (HSD) tests to identify significant differences between cohorts.

Survival analysis.— We used Cormack–Jolly–Seber (CJS) open-population mark–recapture models in Program MARK to estimate the apparent survival of Humpback Chub (φ), defined as the probability that an individual fish was present and alive in the study area (true survival and emigration are confounded), and the probability of capture (p) by using an encounter-history matrix for the PIT-tagged individuals (White and Burnham 1999). In the study of population regulation, survival estimation is advantageous in that the model assumptions are less stringent when compared with those that are structured to estimate abundance. The assumption of individual homogeneity in capture probability is often violated in the field for abundance estimation (Lebreton et al. 1992). The assumptions of the CJS models include that tagged fish are representative of the population, tag loss is nonexistent, and survival of tagged and untagged fish is homogenous.

Using the AIC_c scores that were generated, we tested combinations of predetermined models to assess the hypothesized time-varying and constant effects of fish size and cohort membership on survival and capture probability (Burnham and Anderson 2004). To assess the effect of fish size on survival and capture probability in Havasu Creek, the TL of individual fish at the time of release, or first encounter for nontranslocated fish, was incorporated into the models as an individual covariate on survival and/or capture probability (Table 2). Variables that may be important to adapting future translocations, including those that are related to cohort size distribution (see Table 1), collection methodology (e.g., larval versus juvenile), and release location were accounted for by cohort membership in the CJS models.

Reproduction and recruitment.— We quantified the reproduction and recruitment of the Humpback Chub through the capture of adults that were in spawning condition (expressing gametes) and the presence of untagged young-of-year, juvenile, or subadult Humpback Chub during the monitoring trips. In addition, the presence of juvenile Humpback Chub that were captured in size-classes that were smaller than those of the translocated fish would indicate fish that were produced in situ. We assumed that Humpback Chub reproduction was either low or nonexistent prior to the translocations due to the absence of juvenile or subadult age-classes during our pretranslocation surveys (Trammell et al. 2012).

RESULTS

Following the initial translocation in June 2011, the number of Humpback Chub that was captured ranged from 109 to 626 per trip (Table A.1), with the highest following the translocation of the greatest number of individuals in 2014 (see Table 1). Of 1,954 PIT-tagged translocated individuals that we released into Havasu Creek, we recaptured 51% of them at least once during the 14 sampling occasions. Considering only Humpback Chubs captured during the first netting pass to avoid double counting during a sampling occasion, captures of untagged fish increased from seven, prior to the first

TABLE 2. Cormack–Jolly–Seber model selection results for the top five models by using AIC_c and the model likelihood analysis in Program MARK for apparent survival (ϕ) and capture probability (*p*) estimates for the mark–recapture sampling of Humpback Chub in Havasu Creek, Grand Canyon, Arizona, 2011–2017. The models that were tested included combinations of covariates including total length (TL) and cohort membership, and they included time varying (*t*) or constant (.) survival and capture probability (survival and capture probability did not differ between intervals or sampling occasions, respectively).

Model	AIC_c	ΔAIC_c	AIC_c weights	Model likelihood	Number of parameters	Deviance
ϕ (cohort) $p(t)$	8,479.19	0	0.45	1	19	8,441.01
ϕ (cohort + TL) $p(t)$	8,480.12	0.93	0.28	0.63	20	8,439.93
ϕ (cohort) $p(t + \text{TL})$	8,481.21	2.02	0.16	0.36	20	8,441.01
ϕ (cohort + TL) $p(t + \text{TL})$	8,482.13	2.93	0.10	0.23	21	8,439.91
ϕ (cohort) p(cohort)	8,578.93	99.74	0	0	14	8,550.83

translocation, to 110 in May of 2018 (Figure 2). We assumed that larger (approximately ≥190 mm TL) nontranslocated fish that were captured from 2011–2014 had immigrated into the stream as adults during equalization flows. We observed increases in other native species across sampling events, with our catches more than doubling for both Speckled Dace and Bluehead Sucker between May 2012 and 2018 (Appendix A.1). Rainbow Trout were relatively rare, and catches declined; however, these trap nets are generally not efficient for monitoring salmonids, relative to electrofishing. Electrofishing is ineffective in Havasu Creek due to its high conductivity.

Abundance

The annual abundance of Humpback Chub gradually increased through 2015 as fish were added through the translocations (Figure 3). After 2015, we observed increases in the abundance of nontranslocated Humpback Chub, although the total plateaued at 284 (within the 95% confidence interval 281 ± 307) in May of 2016 (Figure 3). All of the translocated cohorts were represented in the final year of the study, and 51% of the total abundance estimate consisted of nontranslocated Humpback Chub (Table 3). Despite the capture of 47 untagged fish, a data collection error in May 2017 did not allow for the inclusion of the untagged fish in the abundance estimate (Figure 2). The range of our capture (0.53–0.93) and recapture (0.21–0.71) probability estimates were relatively high across all of the two-pass, closed capture sampling events, and the top models that were selected by using AIC_c included varying capture and recapture probabilities across cohorts only in 2012 and 2014 (Table 3).

Growth

We observed differences in the growth rates across the translocated cohorts in first-year summer seasons ($F = 128.7$, df = 4, $P < 0.001$) and winter ($F = 58.35$, df = 4, $P < 0.001$), and summer growth was greater than winter growth (Figure 4). We observed the highest growth rates for the 2011 cohort during both the summer and winter periods (Tukey's HSD test: $P < 0.001$, Figure 4) when the released fish were of generally smaller size (see Table 1). We observed the lowest summer growth rates for the 2014 cohort, which is when we translocated the greatest number of fish (two separate events 1 month apart; Tukey's HSD test: $P < 0.001$; Figure 4). The average growth rate for all of the individual fish combined was 0.32 mm/d (range = 0.03–0.78) in summer and 0.07 mm/d (range = <0.001–0.28) in winter. Aside from the 2011 cohort, the mean winter growth for all of the other cohorts was <0.10 mm/d, while the mean growth rates for all of the cohorts exceeded 0.20 mm/d during summer.

Survival

In Havasu Creek, the apparent survival rate for Humpback Chub varied between cohorts and nontranslocated and translocated fish but not necessarily across time (Figure 5, Table 2). The estimates for the probability of recapture from the open-population model (i.e., the probability that an individual tagged fish would be captured during a seasonal sampling event on either netting pass) ranged from 0.48 to 0.89 (mean = 0.68), and annual survival rates ranged from 0.23–0.56 among cohorts (Figure 5). Among those tested, we found that the CJS model with the lowest AIC_c score included time-varying capture probability and survival estimates varying across cohorts (Table 2). The next most parsimonious model, which differed little in AIC_c score, suggesting almost equal support (ΔAIC_c <1; Burnham and Anderson 2002), included the individual TL covariate, indicating that larger fish had greater rates of survival (Figure 5). The time-varying survival models without cohort effects received no support. Cohort-specific survival was highest among the 2014 and 2011 cohorts and lowest in the last two cohorts that were released in Havasu Creek and the nontranslocated fish (Figure 5).

Reproduction and Recruitment

We first observed reproductively mature, translocated male Humpback Chub in spring of 2012, and we observed females expressing gametes in spring of 2013 and then

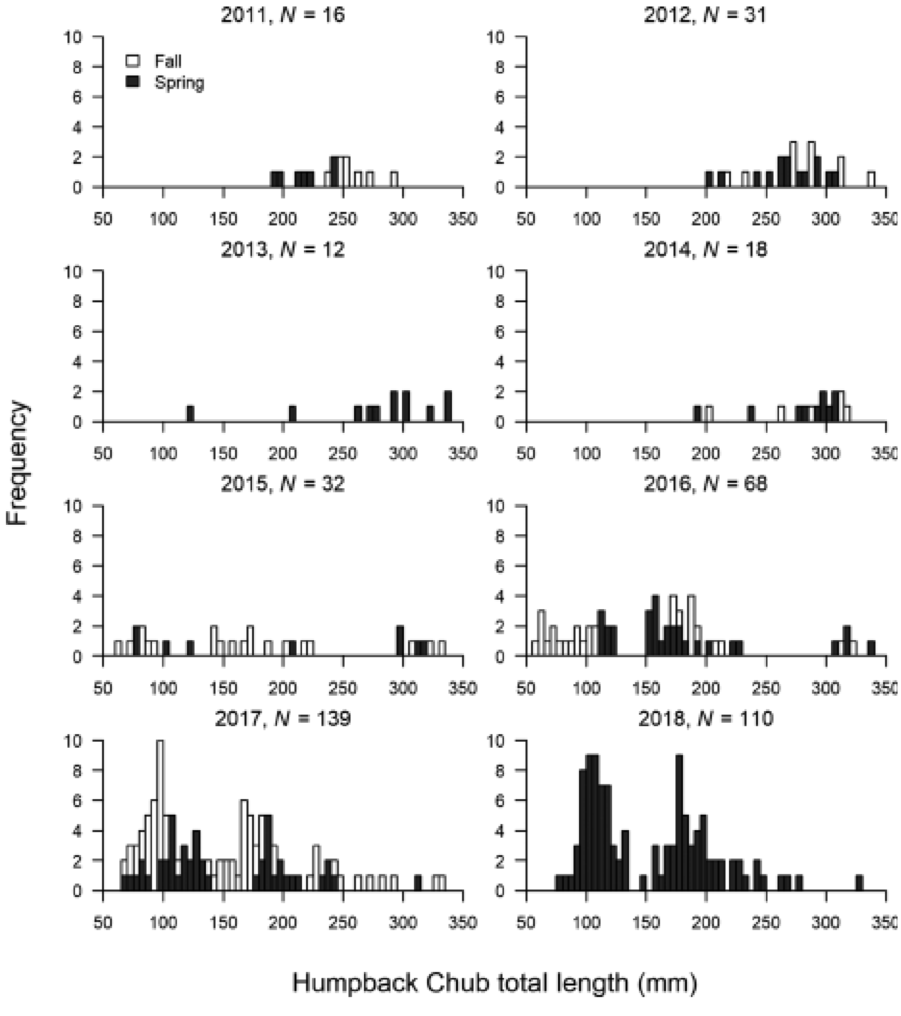

FIGURE 2. Size structure of nontranslocated Humpback Chub (adult immigrants and those that were produced in situ) that were captured during fall (white bars) and spring (first pass only; dark gray bars) sampling trips by year in Havasu Creek, 2011–2018. There are no fall data for 2013 due to cancellation of the sampling event as a result of the U.S. federal government shutdown, and only spring data are included for 2018 (the end of the study).

every spring thereafter. The minimum and median size of the males and females that were in spawning condition was 137 and 156 mm TL, and 200 and 217 mm TL, respectively. These spawning fish were likely minimum age-2 fish, based on observed growth rates and length-frequency histograms (Figure 2). We captured between one and three nontranslocated, reproductively mature Humpback Chub per trip during the 2012–2015 spring sampling events, and from 2016 through 2018 we captured 6, 10, and 16, respectively. Our first observations of juvenile Humpback Chub that were produced in situ were in May 2013, with captures of two untagged juveniles (which measured 121 and 127 mm TL). Then, untagged young-of-year, juvenile, and subadult Humpback Chub were consistently captured annually beginning in 2015 (Figure 2). A minimum of four age-classes of nontranslocated Humpback Chub were evident by 2017 (Figure 2), including mature individuals that were in spawning condition, confirming recruitment to maturity.

DISCUSSION

Our study demonstrates the successful establishment of a reproducing population of an endangered "large-river" fish in a smaller tributary through translocations. Given the limited suitable habitat in the degraded segments of many large rivers, this suggests that tributaries in protected areas may provide important opportunities for habitat conservation and endangered fish recovery (Spurgeon et al. 2015b; Laub et al. 2018). Laub et al. (2018) suggested that the natural flow and thermal regimes in smaller Colorado River tributaries could support the ecological processes—which have been severely altered and are more difficult to restore in main-stem rivers—that are

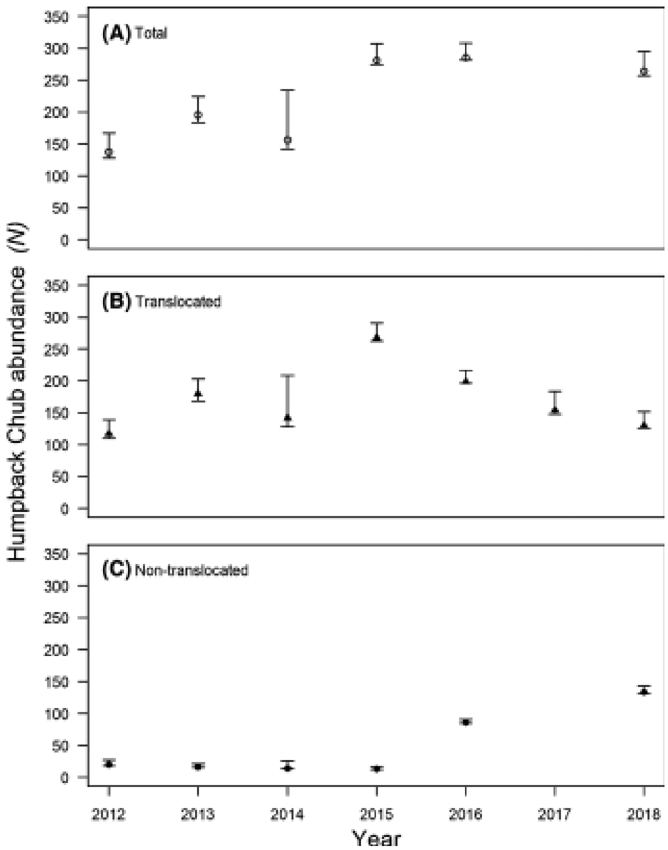

FIGURE 3. Trends in abundance of (**A**) total, (**B**) translocated, and (**C**) nontranslocated Humpback Chub between 2012 and 2018, estimated by using closed-population mark–recapture models. In 2017, no non-PIT-tagged fish were included in the estimate due to a data collection error.

necessary for the maintenance of large-river species. While we must recognize recent exceptions, such as the resurgence of native fishes in much of the Colorado River in Grand Canyon (Kegerries et al., in press), climate change is expected to further constrain streamflow (Udall and Overpeck 2017), which could accelerate the replacement of native fishes by nonnative species (Ruhí et al. 2016). Havasu Creek has considerably smaller discharge than the suggested thresholds for tributaries with conservation potential for large river fishes (~25 m^3/s; Laub et al (2018)), but flows and water temperatures are relatively unimpaired, exhibit characteristics that are consistent with those of spring-fed perennial arid-land rivers, and are reliable and consistent during base flows (Melis et al. 1996).

The large-magnitude monsoonal floods that were frequent during our study period did not appear to limit the survival of translocated fishes, but they may have provided an advantage for native fishes that evolved under frequent disturbance regimes (e.g., see Meffe and Minckley 1987; Poff and Ward 1989). Salmonids that are present in the Colorado River and are known to prey upon or potentially compete with Humpback Chub (Marsh and Douglas 1997; Yard et al. 2011; Whiting et al. 2014; Spurgeon et al. 2015a) may be sensitive to tributary flow regimes that differ from those in their native range (see Fausch et al. 2001; Cattanéo et al. 2002; Dibble et al. 2015). The successful establishment of Humpback Chub in Havasu Creek may be partially attributed to the rarity of invasive fishes, as newly translocated fish and offspring would face less competition or predation pressure (Olden et al. 2008; Whiting et al. 2014; Spurgeon et al. 2015a). Indeed, the presence of nonnative fishes in translocation sites is a common cause of failure (Al-Chokhachy et al. 2009; Cochran-Biederman et al. 2015). No reproduction was observed in Shinumo Creek, where Humpback Chub translocations were conducted between 2009 and 2014 (Spurgeon et al. 2015b) and abundant Rainbow Trout and translocated Humpback Chub occupied a similar trophic position (Spurgeon et al. 2015a). While juvenile Humpback Chub in Shinumo Creek survived and grew at rates that were comparable to those of juveniles in the LCR, emigration rates were high (Spurgeon et al. 2015b) and ultimately a 2014 fire and subsequent flooding extirpated Humpback Chub from Shinumo Creek (B. D. Healy and E. C. Omana-Smith, personal observations; National Park Service, unpublished data). Aside from negative interactions with trout, habitat differences could explain these divergent outcomes. The base flow in Havasu Creek is considerably greater than that in Shinumo Creek, possibly supporting a higher carrying capacity (Pine et al. 2013) and providing greater high-volume pool habitat as refuge during flooding.

The growth and survival rates of Humpback Chub in Havasu Creek were comparable to or higher than those that have been published for juveniles of the same age in other populations. The summer growth rates of the fish in Havasu Creek exceeded those that have been reported in the LCR (0.17–0.31 mm/d; Dzul et al. 2016), allowing juveniles to reach maturity at an accelerated rate. We found that the individuals in the 2011 cohort exhibited the highest growth rates, and some were in spawning condition only one year after release (as age-2 fish), compared with the 3–4 years that is required for fish to reach maturity in the LCR (Yackulic et al. 2014). The survival rate of the cohorts that were translocated to Havasu Creek between 2011 and 2014 ranged from 0.40 to 0.56, which was approximately double the rates of two out of three of the cohorts in Shinumo Creek (range = 0.22–0.41, Spurgeon et al. 2015b). The survival rate of all of cohorts in Havasu Creek (≥0.23) also met or exceeded the estimates for five subadult cohorts in the LCR (see Dzul et al. 2016). These higher growth and survival rates could be explained by hatchery rearing and parasite treatment that would provide a greater advantage over rearing fish in the LCR. Compromised survival would be expected in the

TABLE 3. Estimates of Humpback Chub abundance (*N*) by cohort and year and capture (*p*) and recapture (*c*) probability based on closed-population mark–recapture models; NT = nontranslocated (including fish that were produced in situ), SE = standard error, and CI = confidence interval.

			95% CI		Capture probability	
Cohort and year	*N*	SE	Lower	Upper	*p* (SE)	*c* (SE)
			2012 abundance			
2011	117	6.68	110	139	0.68 (0.07)	0.69 (0.05)
NT	20	1.79	18	27	0.68 (0.07)	0.21 (0.11)
			2013 abundance			
2011	65	2.94	61	74	0.68 (0.03)	0.68 (0.03)
2012	114	5.49	107	130	0.68 (0.03)	0.68 (0.03)
NT	16	1.24	15	21	0.68 (0.03)	0.68 (0.03)
			2014 abundance			
2011	32	8.39	26	69	0.53 (0.20)	0.71 (0.20)
2012	32	0.43	32	35	0.93 (0.05)	0.67 (0.09)
2013	77	7.51	70	104	0.63 (0.10)	0.71 (0.06)
NT	14	2.21	13	26	0.71 (0.20)	0.40 (0.15)
			2015 abundance			
2011	18	0.48	18	21	0.83 (0.03)	0.65 (0.03)
2012	23	0.59	23	26	0.83 (0.03)	0.65 (0.03)
2013	37	0.96	36	41	0.83 (0.03)	0.65 (0.03)
2014	190	3.95	185	202	0.83 (0.03)	0.65 (0.03)
NT	13	0.85	12	17	0.83 (0.03)	0.65 (0.03)
			2016 abundance			
2011	11	0.42	11	14	0.88 (0.02)	0.66 (0.03)
2012	8	0.36	8	10	0.88 (0.02)	0.66 (0.03)
2013	19	0.56	19	22	0.88 (0.02)	0.66 (0.03)
2014	77	1.19	76	82	0.88 (0.02)	0.66 (0.03)
2015	83	1.24	82	88	0.88 (0.02)	0.66 (0.03)
NT	86	1.17	85	91	0.88 (0.02)	0.66 (0.03)
			2017 abundance			
2011	4	0.52	4	7	0.76 (0.05)	0.33 (0.04)
2012	1	0.26	1	3	0.76 (0.05)	0.33 (0.04)
2013	10	0.80	9	13	0.76 (0.05)	0.33 (0.04)
2014	80	2.91	76	89	0.76 (0.05)	0.33 (0.04)
2015	8	0.75	8	12	0.76 (0.05)	0.33 (0.04)
2016	51	2.14	49	59	0.76 (0.05)	0.33 (0.04)
NT[a]	32	1.59	30	38	0.76 (0.05)	0.33 (0.04)
			2018 abundance			
2011	5	0.45	5	8	0.81 (0.33)	0.63 (0.33)
2012	1	0.20	1	2	0.81 (0.33)	0.63 (0.33)
2013	8	0.58	8	11	0.81 (0.33)	0.63 (0.33)
2014	69	1.86	67	75	0.81 (0.33)	0.63 (0.33)
2015	7	0.54	7	10	0.81 (0.33)	0.63 (0.33)
2016	39	1.34	38	45	0.81 (0.33)	0.63 (0.33)
NT	134	2.87	131	143	0.81 (0.33)	0.63 (0.33)

[a]Only includes PIT-tagged fish and no young-of-year.

heavily parasite-infected fish of the LCR (reviewed in Campbell et al. 2019). Individual growth is critical to the survival and reproductive fitness of fish, and the lack of juvenile rearing and recruitment to maturity in the colder postdam waters of the Colorado River (Robinson and Childs 2001; Yackulic et al. 2014; Van Haverbeke et al. 2017) was thought to limit the population in Grand Canyon (Valdez et al. 2000; Trammell et al. 2012). For

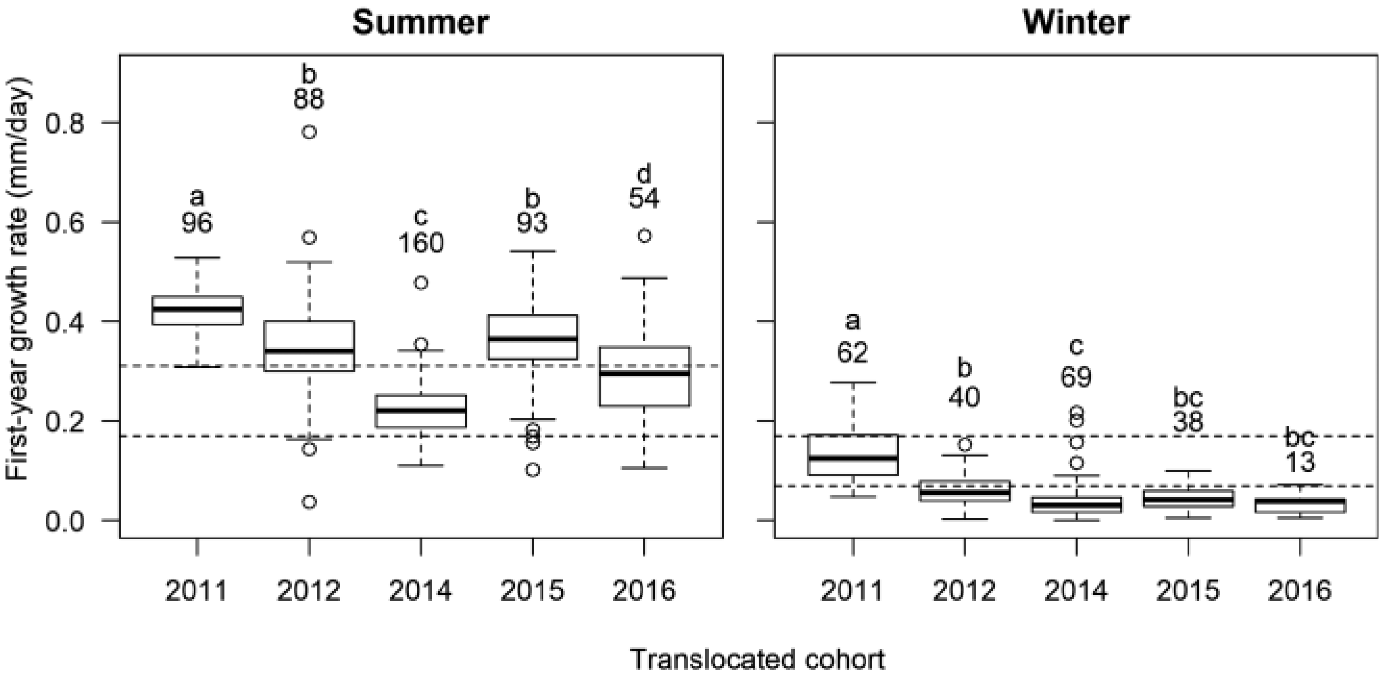

FIGURE 4. First-year absolute daily growth rates for summer (May–September) and winter (October–April) seasons by translocated cohort in Havasu Creek between 2011–2016 compared with the range of published growth estimates for juvenile Humpback Chub in the Little Colorado River, Grand Canyon, Arizona (dashed lines, Dzul et al. 2016). The boxplots indicate median values, interquartile range, and outliers (circles). No growth calculations for the 2013 cohort were possible due to the government shutdown-related cancellation of the fall 2013 sampling trip. The sample sizes are listed above the boxplot for each cohort, and the letters indicate similarity ($P < 0.05$, Tukey's HSD test) among pairwise comparisons of cohort-specific growth rates within a season.

example, Yackulic et al. (2014) suggested that cold-water-suppressed growth would double the time that is required for a juvenile Humpback Chub to reach maturity, reducing the probability of survival to adulthood by approximately 40% through prolonged exposure to predation risk. Our results suggest that population-viability analyses that model the predicated successful establishment of Humpback if survival rates met or exceeded those of fish in the LCR appear to be confirmed (Pine et al. 2013).

Management Implications

The establishment of a reproducing population of an endangered and endemic fish in the Colorado River through translocations is a significant milestone in recovery given that successes are few and require intensive management (e.g., mechanical suppression of invasive fishes; Mueller 2005; Franssen et al. 2014; Healy et al. 2018). Recent status reviews of Humpback Chub recommended down-listing of the species, citing the newly established Havasu Creek population as one of several justifying reasons (USFWS 2018a). Nonetheless, we caution managers against overstating the long-term viability of this population. As observed in Shinumo Creek and in a distinct, upstream reach of the LCR where Humpback Chub were translocated (Van Haverbeke et al. 2013), disturbances can extirpate new populations. Isolated populations, which are valuable to conservation by provision of redundancy and often protected from invasions, are no less vulnerable than fragmented source populations are (Fausch et al. 2009). Postdam isolation from the Colorado River due to flow regulation (i.e., suppressed high flows) combined with severe flooding in the 1990's (Melis et al. 1996) may explain the pretranslocation absence of a self-sustaining population of Humpback Chub from Havasu Creek.

Small populations may also be at greater risk of extirpation as a result of genetic drift and inbreeding, requiring additional management to maintain genetic diversity (Mills and Allendorf 1996). Our abundance estimates and trends in growth rates are suggestive of density dependence. As reproductive rates appeared to increase, abundance leveled off and the minimum and maximum growth rates were evident in the largest cohort released (2014) and when abundance was lowest (2011), respectively, suggesting limitations in carrying capacity. Further, the apparent survival of later cohorts was significantly lower than at the outset of the translocations. A change to larval collections following recommendations in Pine et al. (2013) that was meant to decrease risk to the donor population or a change in the release location for the 2015 and 2016 cohorts could also have limited apparent survival. Larval collections could reduce the fitness of the cohorts by enhancing the survival of cohort members that may not

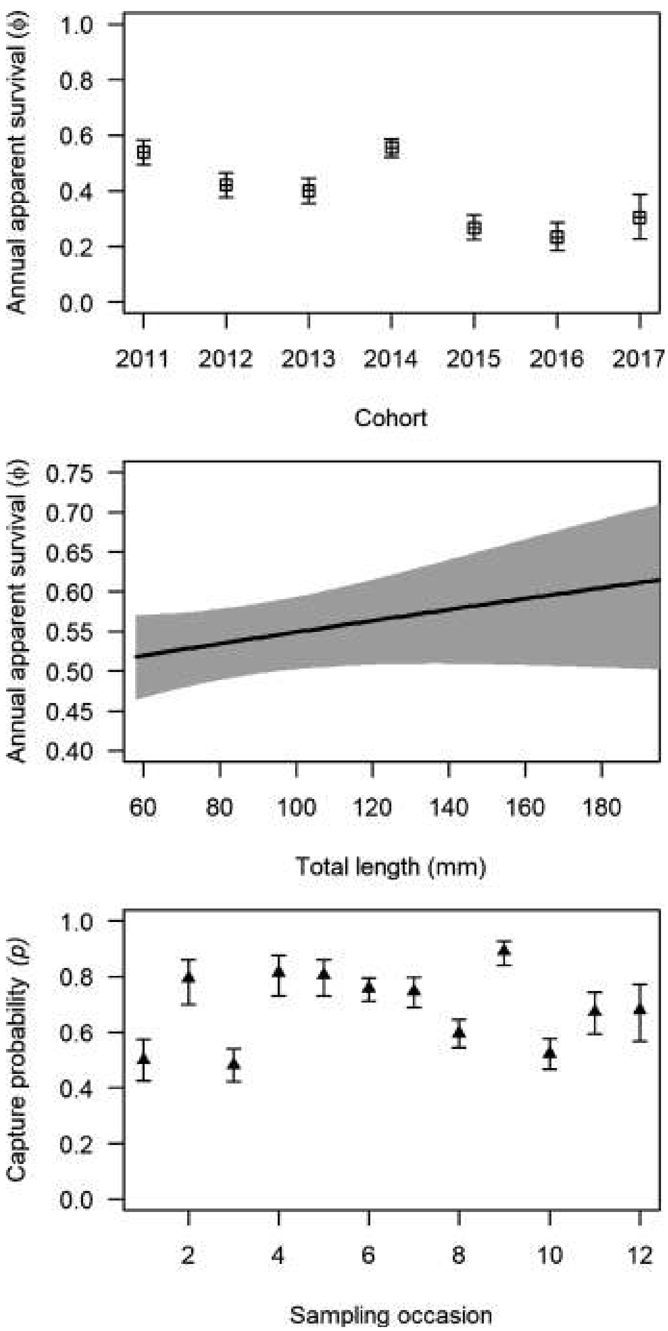

FIGURE 5. Apparent survival of the Humpback Chub that were translocated to Havasu Creek by translocated cohort and nontranslocated fish (NT) based on Cormack–Jolly–Seber modeling. The top model selected by using AIC_c included time- (lower panel) and cohort-varying (top panel) capture probability and apparent survival. The second-most supported model is the relationship between total length at release or first capture (nontranslocated fish) and annual apparent survival of Humpback Chub (middle panel).

have survived selective bottlenecks at larval life stages in the wild. The lower apparent survival could also be indicative of density-dependent emigration. Nevertheless, translocated fish that have dispersed from Havasu Creek have been recaptured in the Colorado River by management and research agencies (the USFWS, Arizona Game and Fish Department, and USGS). These potentially contributed to the recently expanding populations in western Grand Canyon (Van Haverbeke et al. 2017; Rogowski et al. 2018), thereby partially fulfilling the conservation goals for the species (USFWS 2011).

The translocated population in Havasu Creek represents a contribution to the recovery of Humpback Chub by enhancing redundancy, but a longer-term commitment to monitoring is essential to determine the self-sustainment of the population, to assess the reasons for success and failure, and to enable the adaptation of translocation methods. Monitoring is also critical to the maintenance of genetic diversity and avoidance of bottlenecks, which may ultimately compromise the long-term persistence of an isolated, translocated population (Williams et al. 1988). A drawback of our study arose that is related to the concurrent adaptation of the collection and release methodologies that confounded the interpretation of the lower apparent survival rates in later cohorts. Plans for additional translocations or adaptations of existing translocation projects could also benefit from a more rigorous quantitative assessment of the environmental drivers of vital rates in the translocated populations and the population dynamics of the preexisting fish community. For example, flood frequency and intensity varied across years and we might expect summer monsoon floods to transport young-of-year Humpback Chub from Havasu Creek, thereby limiting recruitment (Robinson et al. 1998; Yackulic et al. 2014). Without additional sampling events and analyses, our understanding of the relative importance of inherent factors, such as flow variability, versus variables that are controllable by managers, such as stocking rates (i.e., accounted for in the “cohort effect”), is limited. We also note that we cannot differentiate between the contributions of Humpback Chub that are produced in situ, adults that immigrated in 2011, and mature translocated fish. However, mature translocated fish were much more abundant in years when large year-classes occurred. Nevertheless, as an example of a successful translocation of endangered species that demonstrates the potential importance of tributaries in the recovery of large-river fishes, our study may help to improve the effectiveness of future recovery actions. This is particularly important when budgets for conservation and the availability of imperiled fishes for translocations may limit opportunities.

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Appendix: Summary of Total Fish Captures by Species

TABLE A.1. Total captures of fishes by species across fifteen sampling occasions including the values from baseline monitoring (Trammell et al. 2012), two-pass samples (sampling regime = 2P), and single-netting passes (1P) by year in Havasu Creek, between 2010 and 2018. The data that were collected during sampling occasions 1–12 were used for the survival estimates for Humpback Chub (see Figure 5).

Sampling occasion	Sample month	Year	Sampling regime	Total fish captures	Humpback Chub	Bluehead Sucker	Rainbow Trout	Speckled Dace
Baseline	Feb	2010	1P	240	0	117	10	113
Baseline	Jun	2011	1P	599	7	51	47	494
1	Oct	2011	1P	512	109	106	28	238
2	May	2012	2P	955	188	222	57	427
3	Oct	2012	1P	765	171	197	15	314
4	May	2013	2P	1,349	271	287	8	640
5	May	2014	1P	742	270	147	3	150
6	Oct	2014	2P	1,289	626	239	5	364
7	May	2015	2P	1,349	427	258	4	489
8	Oct	2015	1P	1,210	293	379	1	502
9	May	2016	2P	1,965	478	336	0	995
10	Oct	2016	1P	1,494	232	412	3	804
11	May	2017	2P	1,806	257	280	1	1,068
12	Oct	2017	1P	1,382	190	365	3	743
13	May	2018	2P	2,335	395	544	5	1,152
	Total			17,752	3,914	3,823	180	8,380