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Evaluation of post-stocking re-encounters of an endangered fish using a large, multi-agency database to inform recovery

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ABSTRACT: Managers frequently rely on conservation hatcheries to maintain declining fish populations in the wild, which is the case for bonytail *Gila elegans*, an endangered species endemic to the Colorado River basin, USA. We used a multi-agency database of stocking, capture, and PIT-tag detections during 2013–2021 across the upper Colorado River basin to assess if re-encounter probability of bonytail varied among seasons, stocking habitats (mainstem, tributary, and off-channel), and with length-at-stocking. Because of previous observations of recaptured bonytail in poor body condition, we tested for differences in condition among stocking habitats. Of 325 054 stocked bonytail examined, 90% were never re-encountered. Most re-encounters (93%) were PIT-tag detections near stocking locations. Re-encounter probability was low regardless of stocking habitat, and 95% of fish were at large for <195 d. The effect of length-at-stocking on re-encounter probability varied among habitats and was positive in mainstem and tributary and negative in off-channel habitats. Slopes of length–weight relationships of recaptured fish differed among stocking habitats. Given consistently low re-encounters of stocked bonytail in all habitats regardless of length-at-stocking or stocking season, we recommend managers consider refining the stocking program to better identify specific factors that affect survival, including stocking fish into intensively managed off-channel habitats which afford greater control of abiotic and biotic conditions than riverine habitats. If stocking continues among multiple habitat types, at a minimum we suggest stocking fish at consistent locations over time to better allow for quantitative assessment and to ensure fish are stocked into water temperatures that align with optimums for growth, recovery-from-handling, and survival.

KEY WORDS: Bonytail · *Gila elegans* · Colorado River basin · Hatchery · Conservation · Survival

1. INTRODUCTION

Riverine fish biodiversity is threatened by multiple stressors including habitat loss and fragmentation, flow and temperature regime alteration, and invasive species (Dudgeon et al. 2006, Reid et al. 2019). For species that experience rapid and widespread decline in range and abundance, conservation hatcheries and stocking are common tools to bolster declining populations of freshwater fish or to establish populations where species are extirpated (Osborne et al. 2020, 2021). The goal of conservation stocking programs is often to create self-sustaining populations (Robinson & Ward 2011). For this to occur, stocked individuals

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at a minimum must survive and persist long enough to reproduce. Assessment of post-stocking condition and survival is often a first step in assessing if stocking is achieving objectives.

Conservation hatcheries and stocking are contributing to the continued existence of multiple endangered species in the Colorado River basin in the southwestern USA. Native fishes in the Colorado River basin have experienced rapid decline in range and abundance following wide-spread habitat loss and fragmentation through water development projects and the establishment of introduced fishes (Holden 1991, Minckley et al. 2003). Bonytail *Gila elegans*, is a large-bodied minnow endemic to the Colorado River basin and listed as 'endangered' under the Endangered Species Act of 1973 (ESA; www.fws.gov/species/bonytail-gila-elegans). Between 1950 and the late 1970s, bonytail were subject to severe declines in population size and range due to alterations of flow and temperature regimes downstream of dams, habitat loss and fragmentation, proliferation of non-native fish, intentional poisoning, and other anthropogenic factors (Holden 1991, Bestgen et al. 2008). Because of the species' rapid decline in the wild, very little is known about bonytail ecology (Valdez & Muth 2005). Of 34 individuals collected from the wild between 1976 and 1988 (Minckley et al. 1989), 11 fish were used to develop a broodstock (Hamman 1985) which ultimately formed the basis of propagation and stocking programs throughout the Colorado River basin. No self-sustaining populations of bonytail currently exist in the wild despite several decades of stocking and proclivity to reproduce successfully in captive settings. Evaluation of bonytail stocking is important to understand if the conservation hatchery program is leading to reestablishing populations, and is an opportunity to increase understanding of the species' ecology.

The Upper Colorado River Endangered Fish Recovery Program (hereafter UCREFRP), a multi-agency collaborative program charged with recovering federally protected fish species of the upper Colorado River basin (upstream of Glen Canyon Dam) in the face of continued water development, began stocking in the mid-1990s to establish 3 populations of bonytail which meet recovery goal demographic criteria (USFWS 2002). Initially, stocking efforts assumed that post-stocking survival of bonytail would be sufficient to establish self-sustaining populations of over 4000 fish each in the Green and Colorado rivers over a period of 6 yr. In the decade immediately following adoption of bonytail recovery goals, very few stocked bonytail were re-captured through UCREFRP field investigations (1996–2014; McKinstry et al. 2015). Most fish that were re-captured had been at large only weeks or months following stocking. Bonytail have since been stocked across the upper basin into main channel, tributary, and off-channel habitats. In the only study to assess bonytail stocking in the upper basin (Bestgen et al. 2008), bonytail survived for ≤4 mo after stocking in the middle Green River from 2002 to 2005. In this same study, fish at large for 4 months were in relatively poor body condition compared to fish recaptured soon after stocking (Bestgen et al. 2008). To attempt to improve post-stocking survival, in 2015 the UCREFRP revised their stocking plan by recommending doubling annual stocking rates and increasing mean lengths of stocked individuals. To date, there has been limited formal analysis of bonytail stocking data, and there is a need to assess factors contributing to post-stocking survival to inform recovery efforts.

Post-stocking survival of bonytail is generally thought to be low, but there is some evidence that survival might differ among stocking habitats. There is evidence of stocked bonytail having successfully reproduced in off-channel habitats along the Green River in 2015–2017, 2019, and 2023 (Bestgen et al. 2017, M. Partlow, Utah Division of Wildlife Resources, pers. comm.). While survival of stocked bonytail appears to be low, identifying differences in survival among stocking habitats could inform efforts to revise the stocking program. Our objective was to evaluate bonytail stocking using data from a multi-agency database with stocking, capture, and tag detection records over 9 yr from 8 rivers across the upper Colorado River basin (hereafter UCRB). We focused our analyses on 2 specific questions. (1) Does the probability of re-encounter (physical re-capture or detection on PIT-tag antenna) over time differ for fish stocked into different habitats and as a function of length-at-stocking and stocking season? (2) Does condition of recaptured bonytail vary with stocking habitat? We expected bonytail stocked into off-channel habitats to have a higher probability of re-encounter over longer time periods because previous evidence suggests stocking into off-channel habitat led to higher percentages of fish surviving longer. We also expected there to be a positive relationship between the probability of re-encounter and the length of fish at stocking, presumably due to increased survival of larger fish (e.g. Marsh et al. 2005, Zelasko et al. 2010, Fonken et al. 2023). Finally, we expected bonytail re-encounter probability to be higher for fish stocked during warmer seasons because bonytail stocked into cooler water could experience additional stress (Kappenman et al. 2012).

2. MATERIALS AND METHODS

2.1. Study area

The UCRB drains parts of Colorado, New Mexico, Arizona, Utah, and Wyoming, before entering Lake Powell, an impoundment that inundates a formerly low-gradient reach of the Colorado River since Glen Canyon Dam closed in 1963 (Fig. 1). Recovery efforts for imperiled fishes in the UCRB (not including the San Juan River basin) rely on management efforts administered through a federal recovery program (the UCREFRP) comprised of managers and researchers representing state, federal, tribal, and private stake-

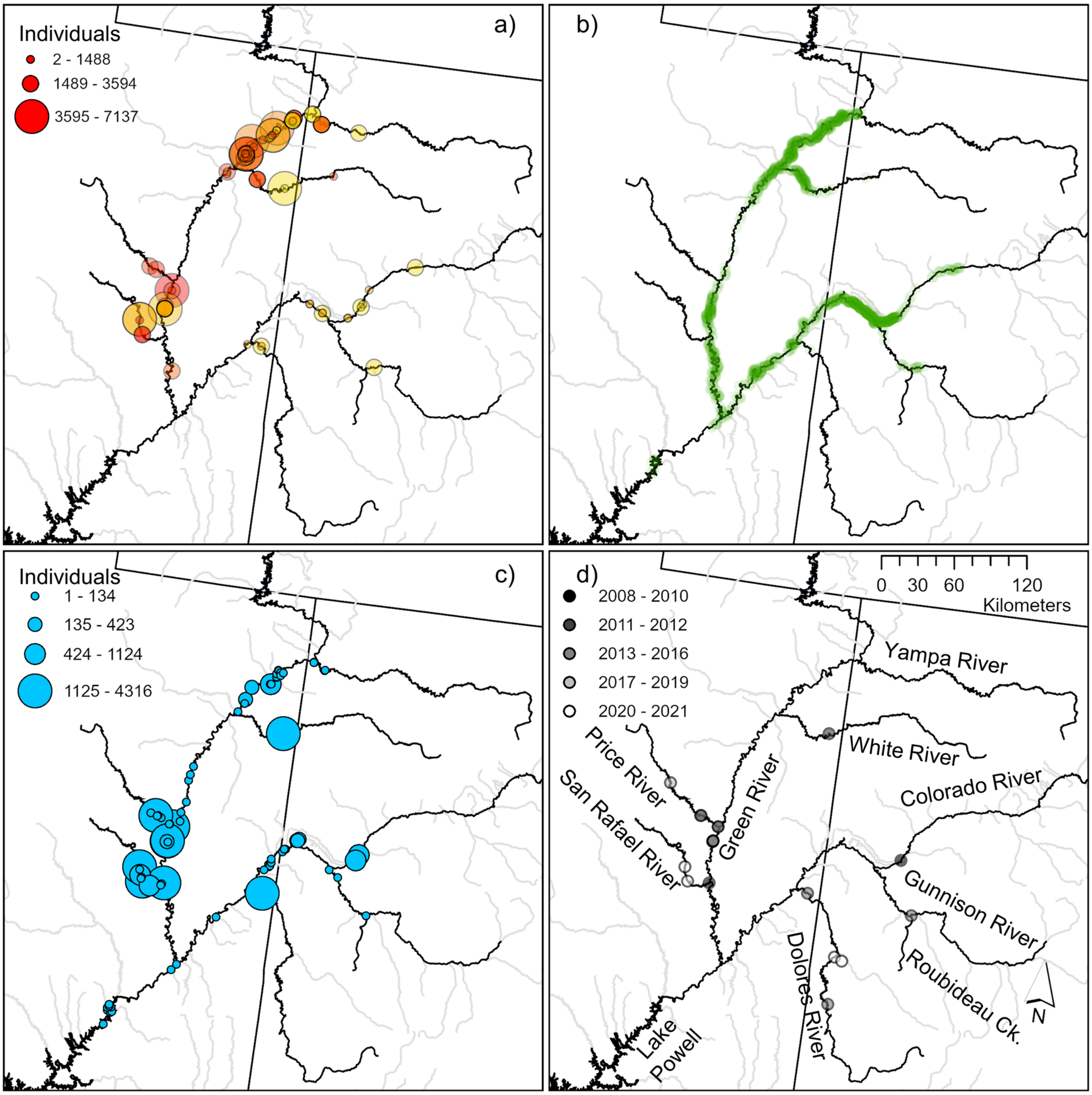

Fig. 1. (a) Stocking locations of bonytail across the upper Colorado River basin between 2013–2021. The size of circles represents the number of individuals stocked each event. Lighter colors represent stocking events closer to 2013. Transparency was added to all points to show overlap. (b) Recapture locations of bonytail between 2013–2021 with transparency added to show overlap. (c) Detection locations of bonytail on PIT-tag antennas. The size of circles represents the number of unique individuals detected. (d) Locations of permanent PIT-tag antennas that were in place between 2013–2021. Darker colors represent antenna locations in operation longer

holders. Activities administered by the UCREFRP include instream flow protection, habitat restoration, non-native fish management, research and monitoring, education and outreach, operating hatchery facilities, and the formation and curation of a centralized tagging database. As part of stocking efforts, most stocked fish are tagged with Passive Integrated Transponder (PIT) tags prior to being stocked, and all UCREFRP research and monitoring protocols require scanning captured fishes for PIT tags and tagging of previously untagged individuals. The UCREFRP, along with the San Juan River Basin Recovery Implementation Program, maintains a centralized database (Species Tagging, Research and Monitoring System, STReaMS; https://streamsystem.org/) of stocking, capture, tagging, and tag detection records from efforts across the UCRB, including the San Juan River and Lake Powell.

2.2. Fish sampling and detection

Fish sampling efforts consistently occur throughout mainstem rivers and some larger tributary rivers in the UCRB. However, effort varies spatially and temporally, and sampling methods vary depending on the goals of individual projects, including sampling (mainly electrofishing) for non-native fish removal, Colorado pikeminnow *Ptychocheilus lucius* and humpback chub *Gila cypha* population estimates, adult native fish monitoring, and various other research projects across more than 1800 km of river (Pennock et al. 2020; https://coloradoriverrecovery.org). For example, total annual electrofishing effort ranged from 267.2 to 3628.7 h in 2013–2021 (mean = 1705.7 h). The use of instream PIT-tag antennas to detect tagged fish has increased throughout the basin at mainstem and tributary river locations (Bottcher et al. 2013, Webber & Beers 2014, Hooley-Underwood et al. 2019; Fig. 1).

2.3. Data download and processing

We downloaded all data on bonytail from the STReaMS database collected between 2013 and 2022 (STReaMS 2023; accessed 2 December 2023). This included stocking, detection, and capture records of fish stocked into the Colorado, Dolores, Gunnison, Green, Price, San Rafael, White, and Yampa rivers and into off-channel habitats along the Green and Gunnison rivers. We focused on this period because use of PIT-tag antennas was becoming more common throughout the upper basin (Zelasko et al. 2022; Fig. 1d), which substantially increased the number of re-encounters (see Section 3). Also, this period included stocking of larger fish (≥250 mm total length, TL) following the most recent UCREFRP stocking recommendations issued in 2015 (UCREFRP 2015). We used fish stocked from 2013–2021 and all detection and capture data of those fish from 2013–2022. We removed any individuals listed as mortalities in stocking records (n = 48), fish with TL at stocking of <100 mm (n = 36), several erroneous records where fish lengths were reported >1000 mm TL (n = 21), and any fish where the PIT-tag number was not reported (n = 59).

2.4. Data analysis

For studies assessing post-stocking survival, it is common to use models to estimate survival while also estimating detection probability, such as mark–recapture models (e.g. Hewitt et al. 2010, Zelasko et al. 2010, 2022). A general guideline for mark–recapture studies is that detection probabilities need to be ≥0.20 to obtain estimates with meaningful precision without extremely high sample sizes of tagged fish (Hewitt et al. 2010). We initially explored the use of mark–recapture models for our dataset, but the extremely low number of re-encountered tagged bonytail despite our large sample size of tagged fish (see Section 3) made it difficult to estimate parameters. For this reason, and because of the unbalanced nature of the data, we opted to use mixed effects models to assess re-encounter probability of bonytail. Because our analysis does not account for imperfect detection, our results of re-encounter probabilities should be considered conservative.

In STReaMS, river water temperature at the time of stocking was only reported for 39% of stocking events. We acquired additional temperature data from the nearest US Geological Survey gage (USGS 2023) where possible, but temperature data for off-channel habitats was unavailable. For this reason, we used stocking season as a proxy for temperature. We classified stocking seasons based on Zelasko et al. (2010): autumn = September and October, winter = November, spring = March–May and summer = June–August. No fish were stocked in December–February. To assess if stocking habitat (mainstem [Colorado or Green rivers], tributary [Dolores, Gunnison, Price, San Rafael, White, and Yampa rivers and Salt Creek], and off-channel ponds and wetlands), stocking season, and TL at stocking (fixed effects) influenced the probability of bonytail being re-encountered (detected or re-captured anywhere in the UCRB), we used generalized linear mixed effects models. We assigned each stocked fish a 1 if it was ever re-encountered (physical recapture or PIT-tag antenna detection) and a 0 otherwise. We also analyzed a subset of data with only the mainstem and tributary habitats using continuous temperature data and report those results in the Supplement because temperature was not a strong predictor of re-encounter probability (Table S1 in the Supplement at www.int-res.com/articles/suppl/n055p055_supp.pdf).

For fish that were re-encountered, we calculated the maximum number of days at large as the difference between their most recent encounter and their stocking date. Mainstem, tributary, and off-channel habitats were monitored with either seasonally maintained or permanent PIT-tag antennas (Fig. 1), and stocking events often occurred near these antennas. This yielded many detections of individual fish shortly after stocking. We filtered the data into subsets by increasing numbers of days at large (i.e. ≥14 d, ≥30 d, ≥90 d, ≥270 d, ≥365 d) to assess how the probability of re-encounter changed with increasing time at large. We assumed a binomial distribution with a complementary log-log link because our response variable was binary (1 = re-encountered, 0 = never re-encountered). We used a complementary log-log link because our data contained many 0's relative to 1's (Zuur et al. 2009). We included stocking season, habitat type, TL at stocking, and an interactive effect of habitat type by TL at stocking as fixed effects in models. We standardized TL to facilitate convergence (scaled and centered on an approximately average size of 260 mm and divided by an approximate SD of 41 mm). We included stocking river, stocking year, and stocking event as random effects to account for variation due to spatial and temporal differences in stocking events and to account for lack of independence of fish from the same stocking event. All analyses were conducted in the R statistical language (R Core Team 2023). We used the lme4 package to run mixed effects models and the car package to test statistical significance (α = 0.05) of fixed effects using Wald's tests (Bates et al. 2015, Fox & Weisberg 2019). We used the MuMIn package to calculate marginal R^2 and conditional R^2 using the delta method, which represent the variance explained by the fixed effects alone and by the fixed and random effects combined, respectively (Nakagawa et al. 2017, Bartoń 2022). We verified that model assumptions were reasonably met using residual plots with the DHARMa package (Hartig 2022).

Previous research documented that bonytail recaptured 4 mo after stocking were in relatively poor condition, weighing an average of 17% less than fish recaptured soon after stocking (Bestgen et al. 2008). We used a linear mixed effects model to test for differences in $\log_{10}$-transformed weight as a function of days at large, $\log_{10}$-transformed length, stocking habitat, and an interactive effect of $\log_{10}$-transformed length and stocking habitat. Transformation of weights and lengths was necessary to meet distributional assumptions. We included stocking year and stocking event as random effects. We removed data from stocking events that reported average TL and weight for each fish in place of individual-specific data. Length and weight data reported for stocked and recaptured fish included several instances of unrealistic values (Fig. S1). We calculated Fulton's condition factor and used condition to identify 'far out' outliers of length and weight using Tukey's fences (Tukey 1977), whereby outliers were any value that fell below Q1−3 × IQR or above Q3+3 × IQR, where Q1, Q3, and IQR are the first quartile, third quartile, and interquartile range, respectively. These individuals were removed from further analysis (Fig. S1). For recaptured fish, we also excluded fish that were at large for <14 d. When interaction terms were statistically significant, we compared slopes with the emtrends function in the emmeans package (Lenth 2023). We calculated marginal R^2 and conditional R^2 as above. We used residual plots to verify model assumptions were reasonably met as described above.

3. RESULTS

Our data filtering resulted in a total of 325 054 PIT-tagged bonytail for analysis, which were stocked across the UCRB between 2013 and 2021 (Table 1). Most fish were stocked into the 2 mainstem rivers, the Colorado River (36.2%) and Green River (31.6%). Approximately 25% of stocked fish were released among the Dolores (6.2%), Yampa (5.1%), White (5.0%), San Rafael (5.0%), and Price (2%) rivers. The remaining 7% were stocked among 6 off-channel habitats. Bonytail were stocked into water ranging from 2.3 to 25.4°C (Table S2). Most fish were stocked into mainstem rivers during summer months (Fig. S2). Stocking in tributary and off-channel habitats mostly occurred in spring, but this varied among individual habitats (Fig. S2).

The overwhelming majority (90%) of stocked bonytail were never encountered again after stocking. Of the 10% of individuals that were re-encountered,

Table 1. Number of bonytail stocked in mainstem and tributary rivers and off-channel ponds or wetlands in the upper Colorado River basin and the mean ± SD of total length at stocking. 'NS' represents no fish were stocked. 'Far out' outliers of total length were removed before summarizing data, which resulted in all data being excluded from tributary stockings in 2015 and 2016 (Fig. S1, www.int-res.com/articles/suppl/n055p055_supp.pdf)

Habitat type	Year	Stocked	Total length (mm) Mean	SD
Mainstem	2013	9209	272.8	27.2
	2014	19737	266.6	32.9
	2015	41023	244.0	21.6
	2016	25111	245.7	27.6
	2017	18720	256.9	30.9
	2018	30272	260.5	22.9
	2019	31125	261.6	28.0
	2020	18253	245.5	36.5
	2021	27012	226.3	45.8
	Total	220462		
Tributary	2013	924	299.0	22.4
	2014	22357	229.5	17.2
	2015	524	–	–
	2016	11524	238.6	18.9
	2017	2830	–	–
	2018	8594	262.3	29.0
	2019	14268	259.9	24.6
	2020	12835	311.9	38.2
	2021	7967	275.9	51.1
	Total	81823		
Off-channel	2013	NS	NS	NS
	2014	NS	NS	NS
	2015	NS	NS	NS
	2016	2715	288.0	32.1
	2017	17733	253.6	21.1
	2018	505	310.9	25.0
	2019	1816	269.2	22.0
	2020	NS	NS	NS
	2021	NS	NS	NS
	Total	22769		
	Grand Total	325054		

93% (29675) were detected by PIT-tag antennas and 7% (2246) were physically re-captured. Most PIT tag detections occurred near stocking locations (Fig. 1a,c). Physical recaptures occurred throughout the UCRB, mostly in mainstem rivers and a few larger tributaries where UCREFRP efforts took place (Fig. 1b). Distributions of time at large were strongly right-skewed (Fig. 2a), and across stocking habitats the median, 75th, and 95th percentile of days at large were 32, 72, and 195 d, respectively.

There was no clear effect of stocking habitat (mainstem, tributary, off-channel) on the probability of bonytail being re-encountered, which was generally low (<0.10) for fish stocked in any habitat type. While mean probabilities were somewhat higher for tributary and off-channel habitats when considering fish at large for ⩾14 , ⩾30 d, and ⩾90 d, probabilities were <0.01 in all habitats for fish at large for ⩾270 d (Fig. 2b). There was a statistically significant interaction between TL at stocking and stocking habitat for re-encounter probabilities for fish at large for ⩾14, ⩾ 30, ⩾ 90, and ⩾365 d ($p \leqslant 0.026$; Table 2). That is, re-encounter probability increased with TL in mainstem and tributary habitats but decreased with TL in off-channel habitats when considering fish at large for ⩾14, ⩾30, and ⩾90 d (Fig. 3). For fish stocked into off-channel habitats, the effect of TL was weak but positive when considering fish at large ⩾365 d (Fig. 3). Re-encounter probability was lowest for fish stocked during winter (November) and was variable among spring, summer, and autumn (Fig. 4). Despite these statistically significant relationships, the fixed effects (season, stocking habitat, and TL) explained a relatively small amount of variation in all models (all marginal $R^2 \leqslant 0.04$), while the random effects (stocking river, year, and event) collectively accounted for more of the variation explained (conditional R^2 = 0.02-0.40; Table 2).

Length–weight relationships differed among stocking habitats both at the time of stocking and when fish were recaptured (Fig. 5). The interactive effect of stocking habitat and TL was statistically significant both at the time of stocking and for recaptured fish (both $p < 0.001$; Table 3). Slopes of length–weight relationships at the time of stocking statistically differed among all stocking habitats (Tukey HSD: all $p < 0.001$; Fig. 5a), coinciding with increases in average length-at-stocking over time. Upon recapture, slopes of length–weight relationships of fish stocked into mainstem and tributary habitats did not differ ($p = 0.910$) but were both higher than the slope for fish stocked into off-channel habitats (both $p < 0.013$). These differences in slopes correspond with 4% heavier fish at 219 mm TL (mean – 1SD), 3% lighter fish at 260 mm TL (mean), and 10% lighter fish at 301 mm TL (mean + 1SD) in off-channel habitats relative to mainstem and tributary habitats respectively (Fig. 5b).

4. DISCUSSION

We identified relationships between length-at-stocking and fish condition that varied among stocking habitats, but this did not appear to result in clear effects on longer-term survival. Bonytail might experience higher levels of stress at temperatures

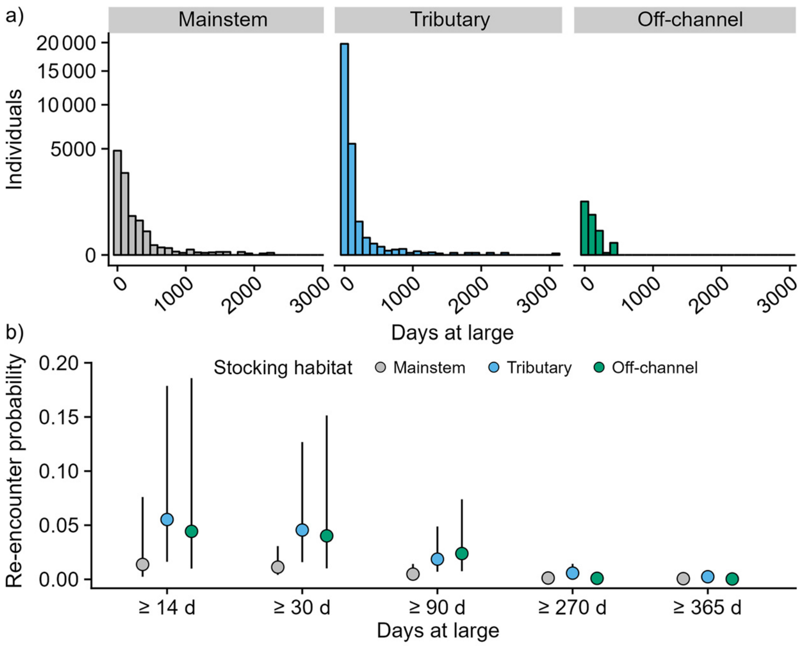

Fig. 2. (a) Histogram of days at large of recaptured or detected bonytail stocked into 3 habitat types from 2013–2021. The *y*-axis is scaled with a square root transformation to better show small counts. (b) Marginal mean estimates (95% CI) from a generalized mixed effects model of re-encounter probability of bonytail (mean total length-at-stocking = 260 mm) stocked into 3 different habitat types for fish at large over increasing lengths of time

Table 2. Results of Wald's tests of generalized linear mixed effects models testing for differences in the re-encounter probability of bonytail at-large for varying numbers of days as a function of season, stocking habitat, total length (TL) at stocking, and the interactive effect of stocking habitat and total length. Marginal R^2 and conditional R^2 represent the variation explained by the model due to the fixed effects alone and the fixed and random effects combined, respectively. **Bold**: statistically significant effects

Time at large	Variable	χ^2	df	p	Marginal R^2	Conditional R^2
⩾ 14 days	Season	5.66	3	0.130	0.04	0.40
	Habitat	1.16	2	0.561		
	TL	92.08	1	**<0.001**		
	Habitat × TL	46.68	2	**<0.001**		
⩾ 30 days	Season	9.19	3	**0.027**	0.04	0.34
	Habitat	7.41	2	**0.025**		
	TL	44.42	1	**<0.001**		
	Habitat × TL	31.47	2	**<0.001**		
⩾ 90 days	Season	14.38	3	**0.002**	0.02	0.18
	Habitat	7.99	2	**0.018**		
	TL	73.12	1	**<0.001**		
	Habitat × TL	11.23	2	**0.004**		
⩾ 270 days	Season	20.53	3	**<0.001**	<0.01	0.02
	Habitat	6.70	2	**0.035**		
	TL	5.21	1	**0.022**		
	Habitat × TL	4.62	2	0.100		
⩾ 365 days	Season	6.67	3	0.083	<0.01	0.02
	Habitat	4.62	2	0.100		
	TL	0.88	1	0.348		
	Habitat × TL	7.30	2	**0.026**		

<14°C (Kappenman et al. 2012), and nearly 28% of stocking events (which would include added stress from handling; UCREFRP 2015) occurred into waters cooler than this. However, the statistically significant effects of season, stocking habitat, and length-at-stocking on re-encounter probability appear minimal given the marginal R^2 was never greater than 0.04. Few bonytail stocked into the UCRB were ever re-encountered past 195 d, which was consistent among stocking habitats and matches previous research that concluded post-stocking survival of bonytail was very low (Bestgen et al. 2008, McKinstry et al. 2015). The decline in the number of individuals re-encountered over time is likely driven by mortality. Some of this decline could be due to emigration, however, it is unlikely that emigration would account for most of this pattern because much sampling takes place annually across >1800 river km to monitor fish populations, and continuously operating PIT-tag antennas are installed in rivers throughout the UCRB. Fish condition varied among stocking habitats whereby fish stocked in mainstem and tributary rivers tended to be heavier per unit length compared to off-channel stocked fish. Regardless of the slight differences in re-encounter probability and weight-at-length relationships among habitats, the probability of re-encountering stocked bonytail beyond 90 d was extremely low in all habitats.

Length-at-stocking tends to be positively related to fish survival. Fish stocked at larger sizes tend to survive at higher rates as larger fish are presumably less susceptible to size-selective predation (Zelasko et al. 2010, Grausgruber & Weber 2020, Hedden et al. 2022). We identified a positive effect of length-at-stocking on re-encounter probability for bonytail in mainstem and tributary habitats, but a negative effect in off-channel habitats. This discrepancy is unexpected but could be explained by mortality of

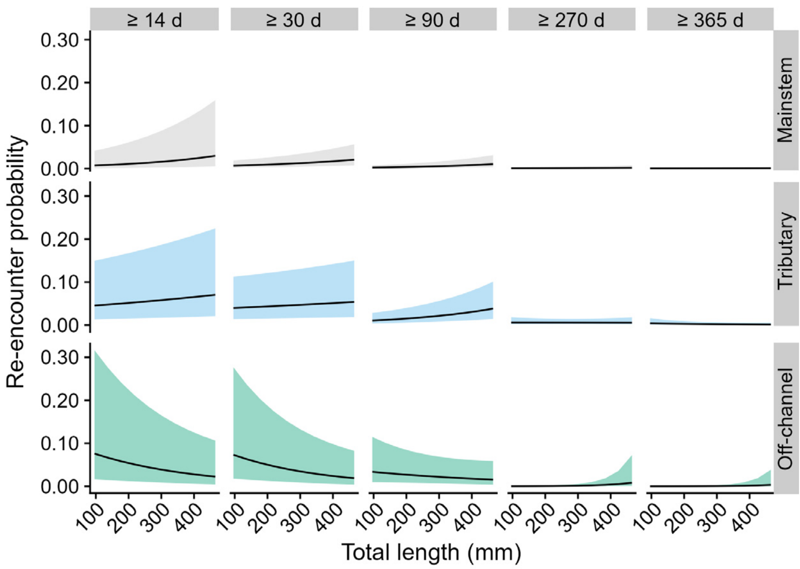

Fig. 3. Re-encounter probability of bonytail stocked into mainstem, tributary, and off-channel habitats as a function of total length-at-stocking. Means and shaded 95% CI were estimated from a logistic mixed effects model

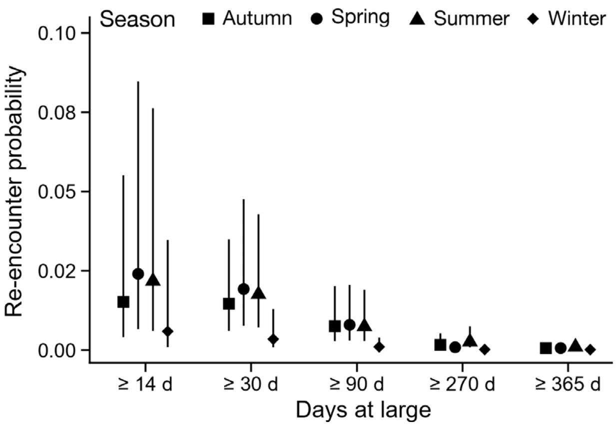

Fig. 4. Marginal mean estimates (95% CI) from a generalized mixed effects model of re-encounter probability of bonytail (mean TL at stocking = 260 mm) stocked in 4 seasons across mainstem, tributary, and off-channel habitats

larger fish in off-channel habitats (due to predation or poor water quality). Regarding mortality as an explanation, larger individuals within a given fish species are frequently more susceptible to mortality from hypoxia and heat stress than smaller individuals (Müller et al. 2023). Such water quality conditions are not uncommon in off-channel wetlands in the UCRB during summer months (M. Partlow, Utah Division of Wildlife Resources, unpubl. data). Also, larger fish are sometimes more frequently consumed by avian predators than smaller fish (Knopf & Kennedy 1981, Shealer 1998, Amirowicz & Gwiazda 2012). Stocking of more bonytail of a range of sizes in off-channel habitats and careful monitoring of water quality and detections within and movements out of these habitats would be necessary to better understand this pattern.

Despite our dataset including over 325 000 stocked individuals and leveraging many PIT-tag antennas and physical sampling efforts across a broad geographic and temporal extent, there were few re-encounters of individuals and the overwhelming majority occurred shortly after stocking (Fig. 2). Because of the low number of individuals encountered in multiple years (Table S3), our analysis differs from assessments of post-stocking survival for other endangered species in the UCRB, such as razorback sucker *Xyrauchen texanus*. For instance, Zelasko et al. (2022) used mark–recapture models to estimate annual survival of 321 233 stocked razorback sucker in the UCRB from 2003–2017 using data from physical recaptures and PIT-tag detections while accounting for imperfect detection. Inclusion of antenna detection data led to substantially higher estimates of first-year post-stocking survival that varied among stocking seasons (mean survival = 0.18–0.57) relative to previous estimates using only physical recapture data (<0.10; Zelasko et al. 2010, 2022). Of stocked razorback suckers re-encountered, 4.3% were physically recaptured, which is approximately 6 times higher than bonytail in the current study despite more bonytail being stocked per year. Although our analysis does not account for imperfect detection, we think our conclusions of low survival are robust given the low number of fish re-encountered beyond more than 1 yr using both physical recapture and PIT-tag detections throughout the entire UCRB (Table S3; Hewitt et al. 2010). Another challenge to isolating specific conditions contributing to successful stocking events is that stockings occurred inconsistently in space or time. Because fish survival appears to be extremely low everywhere, this point might be less important in the present study. However, stocking fish in standardized locations and seasons among years would improve future efforts to identify specific factors contributing to fish survival.

While there is no evidence that stocking bonytail in the UCRB is leading to established populations as described in the 2002 Recovery Goals (USFWS 2002, 2019), there is evidence that fish are successfully using off-channel habitats to reproduce. Bestgen et al

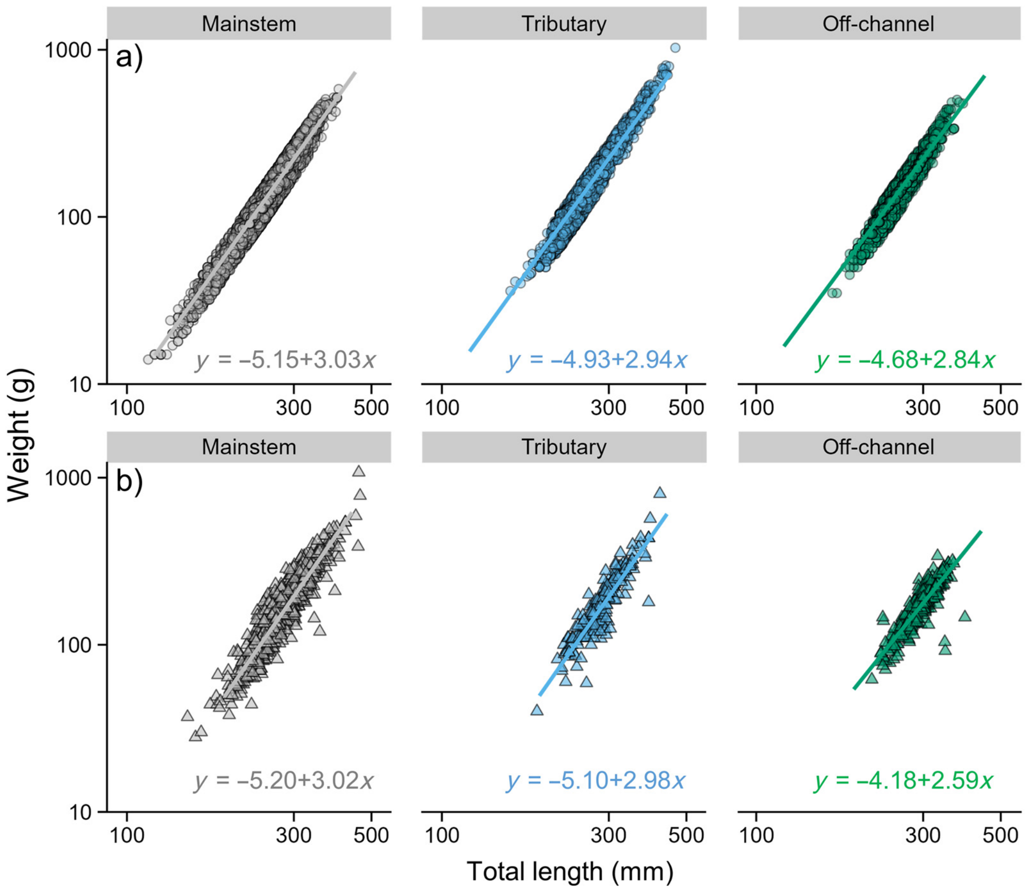

Fig. 5. (a) Length–weight regression for bonytail at stocking (n = 88821) and (b) for recaptured fish from 3 habitat types (n = 1633). The *y*- and *x*-axes are scaled with a $\log_{10}$-transformation and transparency of points was adjusted to show overlapping points. Equations are from linear mixed effects models with fixed effects of $\log_{10}$-transformed total length and random effects of stocking year and stocking event

Table 3. Results of linear mixed effects models of $\log_{10}$-transformed weight (g) as a function of $\log_{10}$-transformed total length (TL; mm), stocking habitat, and their interactive effect at the time of stocking and for recaptured fish. Marginal R^2 and conditional R^2 represent the variation explained by the model due to the fixed effects alone and the fixed and random effects combined, respectively. **Bold**: statistically significant effects

Model	Variable	χ^2	df	p	Marginal R^2	Conditional R^2
Stocking	TL	1 628 264.79	1	**<0.001**	0.93	0.97
	Habitat	4.23	2	0.121		
	Habitat × TL	744.43	2	**<0.001**		
Recapture	TL	9198.76	1	**<0.001**	0.86	0.89
	Habitat	6.80	2	**0.033**		
	Habitat × TL	17.03	2	**<0.001**		

(2017) documented the first instance of bonytail reproduction and survival of wild-spawned fish to at least several months of age. Low numbers (2–600 fish) of age-0 wild-spawned bonytail were discovered in 2 off-channel wetlands in the Jensen-Ouray reach of the Green River in 2015 (Stewart Lake, Johnson Bottom) and in 2016, 2017, 2019, and 2023 (Stewart Lake) and were determined to be the result of spawning activity within the wetland habitats (Schelly et al. 2016, Staffeldt et al. 2017, Partlow et al. 2019, Hyder & Partlow 2023). There are numerous additional examples of bonytail stocked elsewhere voluntarily entering floodplain wetlands presumably during spring peak-flow periods, including fish which had been stocked years prior to their recapture in wetlands (e.g. Jones et al. 2017, Smith & Beers 2019). Although we found no long-term (>90 d) differences among stocking habitats in the probability of re-encountering stocked fish, evidence of wild spawning activity in off-channel habitats suggests that wetlands and ponds could still play a role in bonytail recovery, as suggested previously (Minckley et al. 2003).

Previous investigations have recognized that off-channel ponds and floodplain wetlands afford opportunities for both research and management towards further recovery of razorback sucker and bonytail (Minckley et al. 2003, Mueller 2006, Marsh et al. 2013a,b, 2015, Bestgen et al. 2017). Discovery of wild-spawned bonytail in Johnson Bottom and Stewart Lake on the middle Green River prompted Bestgen et al. (2017) to conclude that expanded use of such habitats could not only lead to greater numbers of wild, acclimated fish but also provide a better understanding of ecological interactions between bonytail, their environment and non-native fishes. Minckley et al. (2003) proposed creation of specially designed and managed (i.e. free of introduced fishes) floodplain rearing ponds which would facilitate production of endangered fish for their ultimate use in repatriating main channel habitats in the lower Colorado River. Key benefits from this approach included relevancy toward conservation goals, protection from catastrophic loss, research opportunities, the ability to manage and maintain genetic integrity (see also Diver et al. 2015), and production of larger and perhaps more adaptable individuals.

5. CONCLUSIONS

Despite statistically significant (but weak) relationships between re-encounter probability and stocking habitat and season, survival of bonytail beyond 1 yr appears low regardless of which habitats are stocked or what time of year stocking occurs across the UCRB. The length of stocked bonytail has generally increased over time following previous recommendations (UCREFRP 2015), and since survival is generally higher among larger fish, the practice of rearing bonytail to larger sizes for stocking should continue. Managers should, however, avoid stocking bonytail during winter months (November–February).

Faced with fundamental information needs about specific factors contributing to poor post-stocking survival, we suggest the UCREFRP consider refining their stocking program to better identify factors that affect survival. First, the current stocking approach seems to function only to keep fish on the landscape and appears to hold little promise for establishment of self-sustaining populations. If this attempt to simply avoid extinction is continued, we suggest stocking fish at the same locations consistently over time and ensuring fish are stocked into water temperatures that align with optimums for growth and recovery from handling (e.g. Kappenman et al. 2012). Such measures could potentially improve post-stocking survival and allow for development of more balanced data sets and thus better quantitative assessment.

Second, the UCREFRP should consider conducting research specifically directed at identifying survival bottlenecks by stocking bonytail into off-channel habitats which are intensively managed for the control or elimination of non-native fish, terrestrial/avian predators, and maintenance of water quality. Whereas our results did not specifically suggest improved survival of fish stocked into such habitats, off-channel habitats are smaller and allow more control of abiotic and biotic factors than mainstem rivers and tributaries. Increased control of conditions within off-channel habitats would allow for experimentally testing the effects of different factors on survival and growth. Also, since bonytail spawn in such habitats, this approach could provide additional benefits in terms of increased production of wild-spawned fish reared in more natural settings than hatchery ponds. For example, wild-spawned fish would experience predator conditioning opportunities (e.g. Ward & Figiel 2013, Solås et al. 2019, Franssen et al. 2021) and natural cover features (e.g. emergent and submerged aquatic vegetation, large woody debris), which are both recommendations in the current stocking plan (UCREFRP 2015).

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