

**ESTIMATION CHALLENGES WITH LARGE-RIVER FISH:
RAZORBACK SUCKER ABUNDANCE AND VITAL RATES IN THE GREEN RIVER, UTAH**

Koreen A. Zelasko and Kevin R. Bestgen

Larval Fish Laboratory, Department of Fish, Wildlife, and Conservation Biology, Colorado State
University, Fort Collins, Colorado 80523, USA

Gary C. White

Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort
Collins, Colorado 80523, USA

June 2020

Larval Fish Laboratory Contribution 217

Recommended citation:

Zelasko, K. A., K. R. Bestgen, and G. C. White. 2020. Estimation challenges with large-river fish: Razorback Sucker abundance and vital rates in the Green River, Utah. Final report to the Upper Colorado River Endangered Fish Recovery Program. Denver Federal Center, Lakewood, Colorado. Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins. Larval Fish Laboratory Contribution 217.

TABLE OF CONTENTS

ABSTRACT	4
LIST OF TABLES	6
LIST OF FIGURES.....	7
INTRODUCTION	8
STUDY AREA.....	10
METHODS	11
Sampling.....	11
Statistical modeling	12
Model effects.....	12
Model selection	13
RESULTS	14
Data summary.....	14
Model selection and parameter estimates.....	15
<i>Survival</i>	15
<i>Abundance</i>	16
<i>Transition probability</i>	16
<i>Capture probability</i>	16
DISCUSSION	17
Abundance.....	17
Total length.....	18
Time at large.....	20
Projected abundance.....	23
Transition probability	24
Capture probability	25
<i>Effects of reach, year, and pass</i>	26
<i>Capture probability vs. abundance</i>	26
<i>Increasing capture probabilities</i>	27
CONCLUSION.....	29
ACKNOWLEDGEMENTS.....	31
REFERENCES	32

ABSTRACT

Freshwater fishes are among the most endangered organisms in the world, particularly long-lived riverine species whose life history and ecological requirements are poorly understood. Such is the case in the Colorado River basin, where habitat alterations and invasive fishes severely diminish distribution and abundance of many species, and their persistence often relies on hatchery augmentation. Massive stocking of hatchery-reared endangered Razorback sucker *Xyrauchen texanus* in streams of the upper Colorado River basin, and resultant increases in captures during sampling efforts for various other species, prompted interest in estimation of population parameters. Using capture data collected during endangered Colorado Pikeminnow *Ptychocheilus lucius* abundance estimation sampling, 2011–2013, we used closed population robust design, multi-state models in Program MARK to estimate abundance, as well as survival, transition, and capture rates of Razorback sucker in three reaches (515 total river km) of the Green River. Only 5.3% of individuals were captured more than once, resulting in low capture probabilities (mean: 0.02, range: 0.002–0.056) and imprecise estimates of other parameters. Abundance estimates increased from 2006–2008 to 2011–2013, due in part to continuous stocking, but varied greatly among years, which was unexpected for this long-lived fish. Survival estimates were most influenced by time at large from stocking to first capture, with higher survival for those at large more than one year, consistent with previous studies that showed fish stocked more recently had lower survival rates. Ultimately, recaptures of Razorback Suckers during Green River Colorado Pikeminnow monitoring were inadequate to produce precise population parameter estimates. However, successful spawning by stocked Razorback Suckers and survival to the juvenile life stage of wild-produced larvae have been documented.

Thus, the potential for self-sustaining populations is increasing, and the need for precise and reliable parameter estimates to evaluate recovery efforts will be essential.

LIST OF TABLES

	Page
Table 1. Razorback Sucker captures ($n = 4,145$) by reach, year, and pass in the Green River, Utah, 2011–2013.....	47
Table 2. Razorback Suckers stocked annually and year of stocking for all individuals ($n = 3,932$) initially captured during this study in three reaches of the Green River, Utah, 2011–2013.....	48
Table 3. Robust design multi-state models to estimate survival rate (S), capture probability (p), transition rate (ψ), and abundance (derived from Huggins model parameters) for Razorback Suckers in three reaches of the Green River, 2011–2013.....	49
Table 4. Recaptures of Razorback Suckers initially captured in three reaches of the Green River, Utah, 2011–2013.....	50
Table 5. Razorback Sucker abundance estimates (\hat{N}), 95% confidence intervals (CI), and coefficients of variation (CV) in three reaches of the Green River, Utah, during two study periods, 2006–2008 (Bestgen et al. 2012b) and 2011–2013.....	51
Table 6. Projected declining abundance trends of Razorback Suckers in the Green River subbasin in the absence of recruitment—the present condition—if stocking were to cease upon expiration of the Upper Colorado River Endangered Fish Recovery Program multi-stakeholder cooperative agreement in 2023.....	52

LIST OF FIGURES

	Page
Figure 1. Map of the upper Colorado River basin, including three study reaches of the Green River, Utah.....	53
Figure 2. Mean daily discharge of the Green River near Jensen, Utah (U.S. Geological Survey gage 09261000), for water years 1947–1964 (pre-impoundment of Flaming Gorge dam), 1965–1999 (post-impoundment), and study years 2011, 2012, and 2013.....	54
Figure 3. Survival rate estimates and 95% confidence intervals (vertical bars) by interval and time at large from stocking to initial capture during this study for Razorback Suckers in three reaches of the Green River, Utah, 2011–2013.....	55
Figure 4. Abundance estimates, 95% confidence intervals (vertical bars), and associated mean annual capture probability estimates (\hat{p}_{mean} , average of sampling passes) for Razorback Suckers captured in three reaches of the Green River, Utah, 2011–2013	56
Figure 5. Model-averaged abundance estimates, 95% confidence intervals (vertical bars), and linear trend line (dotted line; $R^2 = 0.92$) for Razorback Suckers captured in the Green River, Utah, 2006–2008 and 2011–2013	57
Figure 6. Simulation results that depict precision (coefficient of variation , CV) and bias of abundance estimates for three true population sizes of fish (N), under four probabilities of capture per pass (p), using three or four sampling occasions.....	58

INTRODUCTION

Recovery actions aimed at improving the status of rare organisms such as habitat alterations, invasive species reductions, and stocking hatchery-reared individuals, require rigorous evaluation of efficacy. Changes in vital rates and abundance are particularly useful to describe population response to external drivers, measure the pace and direction of recovery, and determine whether management actions are achieving the desired species response. Such population information is often collected via capture-mark-recapture studies but can be difficult to obtain when organisms are widely dispersed, are rare, and occur in difficult to sample and spatially extensive habitat. Such is the case with endangered Razorback Sucker *Xyrauchen texanus*, a large-river catostomid endemic to the Colorado River basin.

Razorback sucker was once widespread and abundant throughout the Colorado River basin, but wild populations are nearly extirpated (McAda and Wydoski 1980; Minckley 1983; Bestgen 1990; Minckley et al. 1991; U.S. Fish and Wildlife Service 2018a; Bestgen et al. In press.). Lower Colorado River basin Razorback Suckers occur mainly in Lakes Havasu, Mohave, and Mead and the Grand Canyon, while those in the upper Colorado River basin (UCRB) occur in the Colorado, Green, and San Juan River subbasins and inflow areas of those rivers to Lake Powell; nearly all are hatchery-reared fish (Minckley 1983; Tyus 1987; Bestgen 1990; Minckley et al. 1991; Modde et al. 1996; Zelasko 2008; Zelasko et al. 2010; Zelasko et al. 2011; Marsh et al. 2015; Kegerries et al. 2017). Wild Razorback Suckers were assumed extirpated in the upper Colorado River and San Juan River subbasins before quantification of any remaining populations was possible (Bestgen 1990; Platania et al. 1991; Bestgen et al. 2002). In the Green River subbasin, abundance of wild adult Razorback Suckers was estimated to be 300–950 individuals during the 1980 to 1992 period (Lanigan and Tyus 1989; Modde et al. 1996) but

declined to less than 100 fish by 2000, and that population was likely extirpated soon after due to lack of recruitment and mortality of old fish (Bestgen et al. 2002). Modified habitat, flows, and water temperatures downstream of dams, channel alterations due to invasive woody plants, and negative invasive species effects are among the main causes for decline of Razorback Sucker (Carlson and Muth 1989; Grams and Schmidt 2002; Olden et al. 2006; U.S. Fish and Wildlife Service 2018a).

To bolster populations of Razorback Sucker throughout the UCRB, hatchery-reared fish were stocked beginning in 1995, with numbers and sizes increasing over time (Burdick 2003; Zelasko et al. 2010; Zelasko et al. 2011), resulting in a cumulative total of > 446,000 to date from several hatcheries (STReaMS 2020). Hatchery fish are surviving in all UCRB subbasins, with higher survival a year or more after stocking (Zelasko et al. 2010), and are reproducing (Osmundson and Seal 2009; Bestgen et al. 2011; Farrington et al. 2016) but with little evidence of recruitment to the adult life stage. Recent increases in Razorback Sucker captures during recurrent, systematic abundance estimation sampling for another endangered species in the UCRB, Colorado Pikeminnow *Ptychocheilus lucius*, prompted interest in understanding if that data was also sufficient to estimate Razorback Sucker population parameters. Here, we use data collected during Colorado Pikeminnow sampling in the Green River subbasin, 2011–2013 (Bestgen et al. 2018), to probe that question and compare results to a similar effort that used data from 2006 to 2008. We also include simulations to illustrate effects of population size, capture-recapture rates, and effort on estimates of abundance. Finally, we make recommendations to improve capture rates going forward, which may be useful to those interested in monitoring abundance of large-river fishes in other locations.

STUDY AREA

The upper Colorado River basin covers portions of Wyoming, Utah, Colorado, New Mexico, and Arizona (Figure 1). Main drainages include the Green River, upper Colorado River, and San Juan River subbasins and the downstream boundary is defined by Lee's Ferry below Glen Canyon Dam, Arizona (Upper Colorado River Basin Environmental Impact Statement Project 1948). The scope of this study is restricted to the Green River subbasin. Channel morphology varies from restricted, high gradient, canyon reaches to wide, braided, alluvial valley reaches (Muth et al. 2000). The region has a semi-arid, high desert climate where streamflow is largely dependent on winter precipitation stored as snowpack in high elevation areas and is regulated by multiple diversion structures and storage reservoirs (Iorns et al. 1965; Van Steeter and Pitlick 1998; Hidalgo and Dracup 2003). Snowmelt runoff produces highest flows in spring to early summer, which decline to base levels in midsummer for the remainder of the year. Since the completion of Flaming Gorge Dam in 1964 in the upper Green River, Utah, spring peak flows of the Green River are lower and summer base flows are higher, on average, than historical levels (Figure 2). Reduced runoff since 2000 has further reduced spring peak flow duration and magnitude, a factor that may affect reproduction and survival of early life stages of several UCRB endangered fish, including Razorback Sucker (Bestgen et al. 2011). However, flow recommendations intended to benefit endangered fishes in the UCRB (Muth et al. 2000), which would restore more natural base and spring peak flows to several rivers in the system, were implemented in 2006 (U.S. Bureau of Reclamation 2006) and revisions have been experimentally applied to further improve status of endangered fishes (Bestgen et al. 2011; LaGory et al. 2012; LaGory et al. In review).

The Green River study area was divided into three reaches where Razorback Suckers are most frequently encountered: from the mouth of Whirlpool Canyon downstream to near the White River confluence (“Middle Green”, river kilometer [RKM] 539.4–396.0 [measuring from its confluence with the Colorado River], excluding 12.9 km in Split Mountain Canyon); from the White River confluence downstream to near Green River, Utah, including Desolation and Gray canyons (“Desolation-Gray”, RKM 395.9–206.1); and from Green River, Utah, downstream to the Colorado River confluence (“Lower Green”, RKM 193.2–0; Figure 1). Sampling was also conducted in the Yampa and White rivers, but because no stocking occurred there and recaptures were relatively sparse, those data were excluded. Hatchery-reared Razorback Suckers have been stocked nearly annually into Middle Green reach (since 1995), Lower Green reach (2003), and the Colorado River subbasin (1995); none have ever been stocked into Desolation-Gray reach.

METHODS

Sampling

Razorback suckers, collected as a secondary objective during capture-mark-recapture sampling for abundance estimation of Colorado Pikeminnow in the Green River subbasin (Bestgen et al. 2007; Bestgen et al. 2010), were captured by boat or raft electrofishing in near-shore habitat each spring, 2011–2013, in each of the three study reaches. Following Pollock’s robust design to allocate sampling effort (Pollock 1982; Pollock et al. 1990), three sampling occasions (“passes”, 7–11 d each) were attempted during each of the three study years. Sampling irregularities included high discharge in 2011, low discharge in 2012, and reverse polarization of electrofishing rafts in Lower Green reach for part of 2013. To allow mixing of marked and unmarked fish, several days elapsed between passes in each reach. All captured

Razorback Suckers were measured (mm TL), weighed (g), scanned for the presence of a Passive Integrated Transponder (PIT) tag, and released within 0.15 km of capture, whenever possible. Because the primary sampling objective was capture of Colorado Pikeminnow, not all of the sometimes-numerous Razorback Suckers were netted and processed.

Statistical modeling

Data were analyzed in Program MARK (White and Burnham 1999) using the closed robust design, multi-state model (Hestbeck et al. 1991; Brownie et al. 1993; Kendall et al. 1995; Kendall et al. 1997; Kendall 1999). Parameters estimated in the primary, open population sampling intervals (years) included: S , probability of survival from the start of one interval to the start of the next (therefore, $1 - S =$ mortality, which in this study included death or emigration from the entire study area) and ψ , probability of transition from one state (river reach) to another. Parameters estimated in the secondary, closed population sampling occasions (passes) included p , probability of initial capture during the sampling year, and c , probability of recapture during a subsequent pass of the same year. Although all Razorback Suckers in this study were essentially “recaptured” after being tagged prior to stocking, “capture” and “recapture” will hereafter denote initial capture and subsequent capture during this 2011–2013 period. Due to paucity of recaptures, recapture probability model structures were all set identical to initial capture probability structures ($c = p$) in lieu of more complex scenarios. To allow inclusion of individual covariates, population abundance (N) was conditioned out of the likelihood using the Huggins closed capture model type (Huggins 1989; Huggins 1991) and, instead, was a derived parameter.

Model effects

Variables hypothesized to affect Razorback Sucker population parameters included river reach, fish length, environmental factors, and time since stocking. The three reaches of the

study area change from braided and alluvial to canyon-bound to alluvial again as the Green River progresses downstream. Associated differences in stocking locations, habitat types, and sampling efficiency prompted inclusion of river reach effects for survival and capture probability rate estimation and use of the multi-state design for transition rate estimation among those reaches. Because transitions are modeled as occurring only annually, within-year reach changes ($n = 5$) were reassigned back to the initial capture reach for that year. The effect of fish length on both capture probability and survival is generally an important feature of capture-recapture studies of fishes; therefore, Razorback Sucker lengths (mm TL) at stocking and at initial capture during the study were included as individual covariates. Squared [TL^2] and cubed [TL^3] terms were incorporated to model the more plausible relationship of survival changing with increasing TL. Year of stocking was included as a surrogate for environmental and hatchery conditions at the time of stocking. Effects of those conditions on subsequent Razorback Sucker survival would be different from those produced by environmental conditions or sampling variation during the study, portrayed simply by time variation within model structures. Year of stocking also allowed calculation of each individual's time at large between stocking and initial capture during the study (< 1 year, > 1 year), similar to an effect in previous studies that found hatchery-reared Razorback Sucker survival rates through the first year post-stocking were lower than in subsequent years (Bestgen et al. 2009; Zelasko et al. 2010; Zelasko et al. 2011).

Model selection

Model selection was conducted with a modified version of Akaike's information criterion (Akaike 1973), denoted AIC_c , which adjusts for small sample size bias (Sugiura 1978; Hurvich and Tsai 1989; Burnham and Anderson 2002) and converges to AIC when sample size is large. Models with lower AIC values are considered more parsimonious and better explanations of the

unknown “truth” that produced the data (Burnham and Anderson 2002). We used confidence intervals (CI) and their overlap among pairs of estimates as an assessment of significance. Model-averaging provided subbasin-wide abundance estimates with measures of precision.

RESULTS

Data summary

The final dataset for parameter estimation consisted of 4,145 capture events of 3,932 unique Razorback Suckers from 2011–2013. Most individuals were only captured once during the study, while 203 were captured twice and 5 were captured three times. Reverse polarization of electrofishing rafts in Lower Green reach during 2013 and difficulties with sampling Middle Green reach during high water in 2011 and low water in 2012 resulted in substantially lower catch rates in those years (Bestgen et al. 2018). Nevertheless, most individuals were initially captured in the downstream Lower Green reach (44%), followed by Desolation-Gray reach (39%) and upstream Middle Green reach (17%; Table 1). A similar pattern emerged for the 208 individuals with multiple captures: nearly 60% ($n = 123$) of recaptures occurred in the Lower Green reach, while only 33% ($n = 69$) and 8% ($n = 16$) occurred in Desolation-Gray and Middle Green reaches, respectively. Of those 208 individuals with multiple captures, only 23 (11%) changed reaches among years of the study, with most captured first in Lower Green then Desolation-Gray ($n = 10$) or Desolation-Gray then Lower Green ($n = 9$). Most capture events (74%) occurred in 2011 and 2012, reflective of lower 2013 captures in Lower Green reach.

Total lengths of Razorback Suckers upon capture averaged 401 mm (range: 182–631 mm) and did not vary greatly within or among initial capture reach. Mean length at stocking for those captured fish was 349 mm TL (range: 177–470).

Of all 3,932 individuals, 31% (range: 11–44% per year and reach) had been at large < 1 year between stocking and first capture in this study, while the remainder had been at large from 18 months to nearly 13 years. The year of stocking for captured Razorback Suckers ranged from 1998 to 2012 (Table 2). The majority (53%) had been stocked in 2009 or 2010, and 90% had been stocked in 2008 or later.

Model selection and parameter estimates

The model with the lowest AIC_c value had 40 parameters and 51% of AIC_c weight (Table 3). Model structure included effects of initial capture reach, study year, sampling pass, and time at large since stocking. The second-best model differed only in the absence of the “at large” effect and was nearly three AIC_c units and five deviance units greater than the top model.

Survival.—Razorback sucker survival rate estimates, \hat{S} , were modeled with seven parameters: six unique interactions among each of the three reaches and two study intervals, plus an effect for time at large since stocking. Due to very low numbers of recaptures between pairs of years in each reach (Table 4), precision of \hat{S} was low, with many 95% CIs nearly spanning zero to one (Figure 3). However, the overarching effect of time at large since stocking was evident. The estimated coefficient for the effect was positive and its 95% CI did not overlap zero (0.96, 0.03–1.89), resulting in higher \hat{S} for Razorback Suckers at large > 1 year in Middle Green and Desolation-Gray reaches. Survival rate estimates were similar between Middle Green and Desolation-Gray reaches from 2011–2012 and were 1.7 times higher when fish were at large > 1 year. The effect was more pronounced from 2012–2013, when estimates for Razorback Suckers at large > 1 year were 2.4–3.8 times higher than those for fish at large < 1 year. The pattern for time at large was not maintained in Lower Green reach survival rate estimates (see DISCUSSION, Time at large).

Abundance.—Estimates of abundance, \hat{N} , were generally highest in upstream Middle Green reach (Figure 4). Annual estimates increased from 2011 to 2012 in all reaches and declined from 2012 to 2013 in Middle Green and Desolation-Gray reaches. Although the 2013 estimate in Lower Green reach is presented for completeness, we doubt the accuracy of the change from 2012 to 2013 given the sampling error and low catch rate of 2013. No estimate is significantly different from others, based on overlapping 95% CIs.

Transition probability.—Razorback sucker transition probability, ψ , estimates were modeled with six parameters, for each of six possible transitions among the three reaches. The probability of remaining in a reach was calculated by subtracting from one the sum of transition rates out of a reach. Given that only 23 reach transitions took place among study years, ψ estimates were not reliable but may illustrate possible trends in movement. Transition probability out of Desolation-Gray reach upstream to Middle Green reach was highest, 0.31, while probability of moving downstream to Lower Green reach was 0.07. Transition probability from the Lower Green reach upstream to Desolation-Gray reach was 0.10. All other ψ estimates were 0.03 or lower.

Capture probability.—Razorback sucker capture probability estimates, \hat{p} , were modeled with 27 parameters, one for each unique combination of three reaches, three study years, and three sampling passes. Mean \hat{p} for the study was 0.02, and mean reach-wide \hat{p} increased from upstream to downstream: 0.01, 0.02, and 0.03 in Middle Green, Desolation-Gray, and Lower Green reaches, respectively. Variation in \hat{p} among reaches and years was considerable, but estimates were always low: maximum per-pass \hat{p} (0.06) was in Lower Green reach and minimum (0.002) was in Middle Green reach, both during the first passes of 2011 (Zelasko et al. 2018).

DISCUSSION

The few recaptures of Razorback Suckers during 2011–2013 sampling and resultant imprecise parameter estimates led us to conclude that data from Colorado Pikeminnow abundance estimate sampling, alone, was not adequate to provide estimates of population parameters useful for management of Razorback Sucker. Despite higher numbers of initial captures during this study, the conclusion was consistent with findings in a similar analysis we conducted using data from Colorado Pikeminnow sampling from 2006 to 2008 (Bestgen et al. 2012b), which produced comparably low capture probability estimates and high parameter imprecision. Abundance estimates derived from similar statistical models were lower for the 2006–2008 period, reflecting fewer years of stocking, and similarly imprecise relative to current estimates. We, therefore, used data simulations to demonstrate the effects of capture probability, effort, and true population size on abundance estimate bias and precision. Below, we compare this study's results to those from the 2006–2008 data analysis, where applicable, and discuss possible reasons for and implications of both.

Abundance

Estimates of Razorback Sucker abundance during 2006–2008 and 2011–2013 time periods were highly variable among years, imprecise, and unreliable (Table 5), largely due to low numbers of recaptures, but nevertheless increased in the later period. Within-year recaptures used to estimate abundance ranged from 0 to 18 in 2006–2008 (Bestgen et al. 2012b) and 1 to 45 in 2011–2013 (Table 4). Relatively precise fish abundance estimates are possible in this system, however. For example, estimates of Colorado Pikeminnow abundance in the Middle Green reach from 2000–2003 had CVs of 9–18% (Bestgen et al. 2007), largely due to more recaptures and higher recapture probabilities.

The variability in Razorback Sucker abundance estimates between years within each study period (e.g., Middle Green from 2006 to 2007, and 2012 to 2013) would not be expected in a relatively large-bodied and long-lived fish species. No relationship was found between the abundance estimate each year of this study and numbers of Razorback Suckers stocked the previous year (Pearson correlation coefficients, r , for Middle Green and Lower Green reaches were -0.52 and 0.04 , respectively). The large swings in annual abundance more likely resulted from low capture probabilities that produced variable abundance estimates (i.e., $\hat{N} = n/\hat{p}$; see *Capture probability vs. abundance*, below) and from low initial post-stocking survival (see *Time at large*, below).

Increased numbers of Razorback Suckers stocked into the Green River starting in 2006 (Table 2, “total” columns) may, however, explain the apparent increase in model-averaged abundance estimates between the two time periods for all reaches of the subbasin combined (Figure 5). Annual Green River estimates of abundance ranged from 2,612–11,111 in 2006–2008 and from 25,482–36,355 in 2011–2013, the wide confidence intervals and imprecise 2013 estimate in Lower Green reach notwithstanding. In addition to more stocked fish, widespread nonnative species control efforts (Breton et al. 2014; Zelasko et al. 2016) and changes in stocking protocols (i.e., increasing mean TL of stocked fish to 300 mm; Shaughnessy 2010) likely improved Razorback Sucker initial survival (Zelasko et al. 2010) and increased abundance between time periods, although effects of those variables were not quantifiable in this analysis (see *Total length*, below).

Total length

Our previous survival analyses for hatchery-reared Razorback Suckers in the UCRB (Zelasko et al. 2010; Zelasko et al. 2011) demonstrated that survival estimates through first

intervals after stocking were positively associated with length at stocking. Thus, for Razorback Suckers in the 2011–2013 dataset, we modeled length at stocking indirectly using initial capture length as a surrogate and directly by compiling stocking records of captured fish. Total length of Razorback Suckers, either at time of stocking or first capture during 2011–2013 sampling, was not a significant effect on any parameter in this analysis. Estimates of the effect were slightly positive, but their confidence intervals included zero. The highest-ranked model incorporating length in the survival structure fell more than four AIC_c points from the top-ranked model and carried only 6% of AIC_c weight (Table 3). Additionally, adding capture length effects to capture probability model structures produced inestimable parameters, further demonstrating a weak effect.

The lack of support for any length effect was surprising, given that length generally affects capture probability of fish (Anderson 1995; Bestgen et al. 2007; Dauwalter and Fisher 2007; Korman et al. 2009; Ehlo et al. 2019) and that TL was important in other analyses of Razorback Sucker survival throughout the Colorado River basin (Marsh et al. 2005; Bestgen et al. 2009; Zelasko et al. 2010; Zelasko et al. 2011; Kesner et al. 2017). Our 2006–2008 investigation of Razorback Sucker population parameters exposed the length effect's waning influence compared to earlier analyses; capture TL appeared in the top-ranked model with a slightly positive effect on capture probabilities (0.007, 95% CI: 0.001–0.012), but did not aid survival estimation (Bestgen et al. 2012b).

Because length did not emerge as an influential effect on Razorback Sucker survival rates or capture probabilities during the 2011–2013 time period, we scrutinized the length data and found that 90% of sucker lengths at capture fell between 325 and 475 mm TL. Survival rates generated for that TL range in an exploratory analysis differed by 11% or less within each time

interval. Similar to lengths at capture, 90% of sucker lengths at stocking fell between 300 and 400 mm TL and over 60% were between 325 and 375 mm TL. Length-dependent survival rate curves generated by the lower ranking models in the current model set exhibited the expected relationship (increasing survival with increased length at stocking), but 95% CIs of all length-effect estimates spanned nearly the entire interval from zero to one.

Our earlier analysis of hatchery-reared Razorback Suckers (pre-2006) allowed for estimation of the length effect on survival and capture probability because it included many years of stocking data (1995–2005) and more fish in smaller length categories (Figure 5 in Zelasko et al. 2009). Protocols have evolved to stock fewer but larger Razorback Suckers (Nesler et al. 2003; Shaughnessy 2010; Integrated Stocking Plan Revision Committee 2015), so TL may have become less influential when estimating population parameters. Furthermore, the few recaptures made during this study hindered our ability to determine if or how fish size (at either stocking or capture) affected survival and capture probability. Nevertheless, differences between lengths at stocking and capture from both time periods were evident. Of Razorback Suckers captured during the 2006–2008 period, only 12% were ≥ 400 mm TL at stocking (adults; U.S. Fish and Wildlife Service 2002), but 36% were ≥ 400 mm TL upon recapture (Bestgen et al. 2012b). Similarly, of those captured during 2011–2013, 4% and 54% were stocked and recaptured, respectively, at total lengths ≥ 400 mm. The differences demonstrate that surviving Razorback Suckers can adapt and grow after being stocked into the Green River.

Time at large

The effect of time at large from stocking to first capture during this study continued to be an influential effect on Razorback Sucker survival. In both Middle Green and Desolation-Gray reaches, Razorback Suckers at large > 1 year before capture during 2011–2013 survived at

higher rates than those at large < 1 year before first capture. Overlapping 95% CIs among pairs of reaches, intervals, and at-large categories (Figure 3), however, preclude meaningful comparison of specific estimates and only allow examination of trends. The pattern of lower survival for Razorback Suckers at large < 1 year before capture in both the Middle Green and Desolation-Gray reaches supports findings from previous studies of the species' post-stocking survival. Marsh et al. (2005) estimated first-year survival to be ≤ 0.26 for most Razorback Suckers stocked in Lake Mohave from 1999–2002, and other tag-recapture studies of stocked Razorback Suckers in the lower Colorado River estimated very low first-year survival (Schooley et al. 2008; Kesner et al. 2017). Razorback suckers of average length (252.5 mm TL) stocked into the UCRB from 1995–2005 survived first intervals at a mean rate of 0.05 (Zelasko et al. 2009). We found similar patterns during the 2004–2007 study period in the UCRB (Zelasko et al. 2011) and 1994–2008 in the San Juan River (Bestgen et al. 2009). The effect was not investigated in our analysis of data from 2006–2008. The pattern of higher survival for Razorback Suckers at large > 1 year before capture in 2011–2013 was not maintained in the Lower Green reach due to relatively few recaptures, particularly in 2013 (Table 4), and the resultant poorly estimated parameters.

The trend of low first-year survival for stocked Razorback Suckers in this study and others was not unexpected, given the relatively benign hatchery environment in which many fish are raised for 1.5–2.5 years prior to stocking: stable or no flow velocity, uniform temperatures, dependable and abundant food, and predator-free habitats may leave fish unprepared for conditions encountered upon release (Suboski and Templeton 1989; Olla et al. 1998). Excessive post-release mortality has been a problem faced by hatcheries for decades (Miller 1954; Flick and Webster 1964; Pitman and Gutreuter 1993; Stahl et al. 1996), and such mortality continues

to plague recent conservation efforts to reestablish declining species in their native ranges (Brown and Day 2002). For example, White Sturgeon *Acipenser transmontanus* stocked into the Kootenai River, Idaho, had first-year survival rates 30% lower than in subsequent years (Ireland et al. 2002; Justice et al. 2009). A Brown Trout *Salmo trutta* stocking experiment in Austrian streams found that hatchery-reared parr of either local or non-local origin were outcompeted by resident, wild fish (Pinter et al. 2017). Hatchery-reared June Sucker *Chasmistes liorus mictus* exhibited a TL-dependent, post-stocking survival pattern similar to that of Razorback Sucker with first year estimates of 0.02–0.03 for fish typically stocked at 200 mm TL (Ehlo et al. 2019). In the same subbasins as Razorback Suckers, hatchery-reared Bonytail *Gila elegans* have such low return rates after being at large > 6 months that post-stocking survival is assumed negligible (Badame and Hudson 2003; Bestgen et al. 2008; Humphrey et al. 2016). Genetic analyses of Razorback Sucker hatchery stocks throughout the Colorado River basin may provide further insight into variable post-stocking survival rates (Dowling et al. 1996; Dowling et al. 2012; Bestgen et al. In press.).

The recently completed revision to Razorback Sucker propagation and stocking protocols in the UCRB (Integrated Stocking Plan Revision Committee 2015) addressed low first-year survival by reducing the number of Razorback Suckers stocked and increasing mean TL from 300 mm to 350 mm. The plan also called for an intensive rearing method (a combination of outdoor ponds during warmer months and indoor rearing in winter to increase growth) and stocking in seasons other than summer, recommendations from Zelasko et al. (2009, 2011). Incidentally, most Razorback Suckers captured during the 2011–2013 period were stocked during 2009, the year with the lowest proportion of summer-stocked individuals (< 0.01) since 2006, a period with relative consistency in numbers of fish stocked.

Projected abundance

High current abundance estimates and higher survival rates after first years post-stocking are adequate to maintain the Green River Razorback Sucker population on the landscape for many years without natural recruitment. However, to demonstrate the contribution of hatchery-reared individuals to maintenance of that population, we used abundance estimates and survival rates from this work and others to simulate the potential response of the species to a possible cessation in stocking. Recovery goal criteria include maintenance of a self-sustaining population of 5,800 adults in the Green River subbasin (U.S. Fish and Wildlife Service 2002). We projected Razorback Sucker abundance after year 2023, when the Upper Colorado River Endangered Fish Recovery Program multi-stakeholder cooperative agreement expires (<https://www.coloradoriverrecovery.org/documents-publications/foundational-documents/2009extension.pdf>), to predict when Green River abundance would fall below the stated criteria if stocking were to cease in the absence of an extended agreement. Applying survival rates from our most robust assessment of stocked Razorback Suckers (0.40 and 0.75 for first and subsequent years post-stocking, respectively; Zelasko et al. 2010) to a hypothetical Green River population of 30,000 fish with no recruitment (this study) indicated that numbers would decline below the recovery level within five years of supposed stocking cessation (2027; Table 6) and to fewer than 300 in another ten years. Thus, to maintain 5,800 individuals, stocking would have to continue in perpetuity but would not address the important criterion that the population be self-sustaining. Our projection demonstrates that, while stocked adults are currently integral to management of the species and stocking is not likely to cease in the near future, natural recruitment of wild-produced Razorback Suckers must be prioritized to achieve recovery goals.

Transition probability

Few annual movements among reaches from 2011 to 2013 precluded meaningful interpretation of transition rate estimates; however, most of those few movements (and highest transition rates) were out of Desolation-Gray reach (total $\psi = 0.38$), and most of those movements were upstream to Middle Green reach (9 of 23 among-year reach changes; Zelasko et al. 2018). Movement by Razorback Suckers to Middle Green reach may be explained by migrations to known spawning areas (Modde et al. 2005). However, the disparity in movement rates among reaches was unexpected, given that no Razorback Suckers were stocked in Desolation-Gray reach and fish captured there from 2006 to 2008 were never recaptured in any reach during those years, implying very low survival. Thus, fish captured in and transitioning out of Desolation-Gray reach must have originated in another reach. In fact, most upstream movement of Razorback Suckers was from Lower Green reach to Desolation-Gray reach during this study (10 of 23 among-year reach changes; $\psi = 0.10$), but very little from Middle Green reach downstream to Desolation-Gray reach (1 of 23; $\psi = 0.03$).

The mainly upstream, albeit few, movements detected in this study contradicted results from 2006–2008, which found no movement among reaches, and our earlier in-depth analysis of Razorback Sucker movement, which found overwhelmingly downstream movement patterns within both the Green River and Colorado River subbasins (Zelasko et al. 2010). That study spanned 12 years of stocking and recapture data, included analysis of within-and among-year movements rather than estimation of annual transition rates, and found most movement (longest distances and highest rates) occurred between stocking and first capture (Zelasko et al. 2009). Both Desolation-Gray and Lower Green reaches are downstream of stocking locations, and the proportions of Razorback Suckers captured each year (2011–2013) that were stocked the

previous year (2010–2012) were higher in those two reaches than in Middle Green reach (Table 2). Thus, stocked fish may have moved (or been swept) downstream before initial spring capture during this study, and then were primarily observed moving upstream between initial and subsequent capture. Regardless, among-year transitions by fish were too few to describe meaningful patterns.

Importantly, transition probabilities estimate movement among study reaches, not movement off the study area. Since apparent survival, S , is the probability of an individual surviving an interval, given that it was alive at the start of the interval and in the study area available for capture, the quantity $1 - S$ represents the probability that individuals either die or emigrate to areas where they are not susceptible to capture. Sampling for this study covered much of the Green River subbasin (515 km) and larger tributaries, but Razorback Sucker encounters during other times of year (Bestgen et al. 2012a; Bestgen et al. 2013) and movement to/from areas not included in this study, like Lake Powell, Colorado River, and San Juan River (Durst and Francis 2016; Albrecht et al. 2018), illustrate the pressing need to incorporate additional data. Stationary antenna arrays, in place throughout the UCRB for years, have been collecting valuable PIT tag encounter data and are being incorporated into additional analyses. The increased encounter data may provide a more accurate representation of true survival and movement patterns for Razorback Suckers through time and space in the UCRB.

Capture probability

Recapture rates of Razorback Suckers (either within- or among-year) were low: 208 (5.3%) of 3,932 individuals from 2011 to 2013 and 71 (7.1%) of 1,004 individuals from 2006 to 2008. Lower recapture rates in 2011–2013 accordingly resulted in lower capture probability

estimates (0.002–0.056) than those from 2006–2008 sampling (0.004–0.070). In this study, we found that capture reach, year, and pass all affected capture probabilities.

Effects of reach, year, and pass.—Capture probability estimates were highest in Lower Green reach (except in 2013 due to equipment malfunction) and lowest in Middle Green reach. The pattern was similar for Colorado Pikeminnow estimates generated from the same sampling effort (Bestgen et al. 2018) and for Razorback Sucker estimates from 2006–2008. The importance of sampling year on Razorback Sucker capture probability in this time period may have been driven by equipment problems (2013) or sampling efficiency challenges during exceptionally high (2011) and low (2012) flow years (Figure 2; Bestgen et al. 2018). Fish behavior (i.e., learned gear avoidance) may also lead to annual variation, depending on the proportion of each year’s catch that was previously captured; however, Bestgen et al. (2017) tested for evidence of such an effect in Colorado Pikeminnow mark-recapture data and found none. Another factor that may have affected capture probabilities among years in this time period was the switch from Smith-Root to ETS electrofishing units to minimize damage to fish caused by potentially harmful waveforms of electricity (Martinez and Kolz 2016). Differences in wave forms and electrofishing power may cause differences in catchability of fish. Biologists noted that Colorado Pikeminnow appeared less stunned and more difficult to net using the new gear, but capture probabilities for Colorado Pikeminnow have declined since 2000 (Bestgen et al. 2018), long before sampling equipment was changed. Similar to year effects, differences among passes can result from sampling efficiency and fish behavior. Variation among reaches, years, and passes is of little consequence, however, when overall capture probabilities are miniscule.

Capture probability vs. abundance.—While capture probability estimates were quite low, the relative size of the difference between some pairs of estimates was substantial and can

dramatically affect other parameters. The influence of capture probability on abundance is clearly illustrated in Figure 4 where the lowest capture probability estimates resulted in inflated and highly imprecise abundance estimates (see Table 5 for % CVs). Annual changes in abundance of the magnitude reported here should not be expected in these relatively large and longer-lived fish. Increasing capture probabilities and their precision results in increased precision of other parameter estimates (Seber 1986; Lebreton et al. 1992), and we demonstrated that principle using data simulations (Bestgen et al. 2012b; Figure 6). With few exceptions, increasing capture probabilities increased precision and reduced bias of abundance estimates, and further improvements were seen in larger populations sampled on more occasions. For example, even in modest-sized populations (e.g., 5,000 animals), precision increased > 50% and bias was reduced to negligible as capture probability increased from 0.02 to 0.05, with either three or four sampling occasions.

Increasing capture probabilities.—One reason for overall low capture probability estimates in most Razorback Sucker studies in the UCRB may be that there is no specific adult monitoring program in place for the species, so data was mostly collected as a secondary objective during Colorado Pikeminnow abundance estimation sampling. Estimates were higher for Colorado Pikeminnow than Razorback Suckers in each reach, year, and pass of the same sampling efforts in 2006–2008 and 2011–2013, even though the Colorado Pikeminnow capture rates in the latter period were among the lowest ever documented (Bestgen et al. 2018), suggesting that Colorado Pikeminnow may be more vulnerable to capture at that time of year.

Future Razorback Sucker parameter estimation would benefit from increasing encounters through a variety of methods. First, more consistent physical sampling focused on Razorback Suckers, as defined by Bestgen et al. (2012b), should be conducted in years when intensive

sampling for other purposes is not occurring. This would ensure that all Razorback Suckers are netted and scanned for PIT tags, a seemingly obvious requirement not always fulfilled because of the large numbers of fish and limited resources. Sampling in spawning areas has been discouraged to avoid disturbance and injury (Muth and Ruppert 1996), but managers should reconsider the restriction, given that abundant larvae are produced in most years (Bestgen et al. 2012b), electrofishing technology has evolved to cause the least harm possible (Martinez and Kolz 2016), and it is an opportunity to capture large numbers of easily accessible fish (including potential wild-produced and untagged adults). Floating PIT tag antennas (Fetherman et al. 2014; Stout et al. 2019) could be employed in tandem with physical sampling of known spawning locations and elsewhere to increase the number of tagged fish detections while avoiding handling stress. Additional passive gears (e.g., fyke nets) could be used during electrofishing passes to increase physical encounters. Finally, because deep and turbid water in the Green River subbasin limits effectiveness of active sampling gear such as electrofishing, incorporating detections from stationary PIT tag antenna arrays would provide valuable encounter data. For example, 530 unique Razorback Suckers were detected by a single array at the Green River canal in 2013 alone (STReaMS 2020), which is nearly 50% of all 2013 capture events using active gear in this study. Furthermore, 93% of Razorback Suckers detected in 2012 and 2013 by antennas at a spawning area in the middle Green River had never been captured by other sampling efforts since being stocked 2 to 13 years prior (Webber and Beers 2014). Razorback suckers are known to travel among the subbasins of the upper Colorado River basin (Durst and Francis 2016; Albrecht et al. 2018), so incorporating the above methods across a broader geographical area would increase encounter probabilities of fish stocked into the Green River subbasin and better reflect true survival.

Examples from other river basins have demonstrated the benefit of employing antenna data. In the lower Colorado River basin, inclusion of PIT tag antenna data increased the low empirical encounter rates of Razorback Suckers and resulted in more precise abundance estimates (Schooley et al. 2008; Kesner et al. 2017). A study of salmonids in the John Day River, Oregon (Conner et al. 2015), found higher precision and lower or equal bias in survival rate estimates when data from PIT tag antennas were incorporated using the Barker model (Barker 1997) compared to Cormack-Jolly-Seber (Cormack 1964; Jolly 1965; Seber 1965) mark-recapture estimates. At a waterfall barrier in the lower San Juan River, New Mexico, 73% of Razorback Suckers encountered in 2017 were detected by antennas but never captured by physical sampling, and 19% of those only physically captured did not have PIT tags (Cathcart et al. 2018). Thus, physical captures and thorough tagging and scanning protocols of Razorback Suckers would still be needed to analyze individual characteristics, such as TL or condition, and to document fish with no tags to monitor potential recruitment. Furthermore, careful consideration should be given to where and when antennas collect data and how that data contributes to parameter estimates prior to inclusion of detections alongside more traditional methods in sampling designs. Nevertheless, obtaining higher capture rates of Razorback Suckers via the multiple, aforementioned methods would increase confidence in vital rate estimates, information which is key to assessing species status and progress toward recovery.

CONCLUSION

The difficulties of estimating vital rates and abundance of rare, large-river fishes are many and demonstrated by the lack of such studies in the literature. We concluded that data collected during Colorado Pikeminnow abundance estimation sampling, alone, resulted in less

than ideal estimates of population parameters useful for management of Razorback Sucker and recommended several approaches to increase capture probabilities to aid the process. However, these intensive sampling programs are costly, and managers will need to weigh the value of increased accuracy and precision of estimates that may be attainable against the costs required to implement them. In 2018, the USFWS recommended downlisting the Razorback Sucker from endangered to threatened status (U.S. Fish and Wildlife Service 2018b) based on relatively imprecise abundance data (Zelasko et al. 2018), in conjunction with sustained survival of and reproduction by hatchery-reared individuals and continued nonnative fish species control efforts. Other important advances to meet life history requirements included fish passage installation to maintain connectivity to spawning areas or adjacent reaches (e.g., Tusher Diversion in the Green River) and flow and floodplain management designed to transport and rear larvae (Bestgen et al. 2011; LaGory et al. 2012). Recruitment potential is, indeed, increasing (LaGory et al. In review), but until the species is self-sustaining and as long as decision-makers continue to use abundance and survival of stocked fish as metrics of recovery, it is imperative to generate reliable population parameter estimates as baseline information. Furthermore, any monitoring of a newly self-sustaining population would require the same level of reliability and would benefit from the recommendations in this study. Managers should always consider what information is most timely and useful to aid decision-making and evaluate if a focus on other life stages or estimators (recruitment of young, population rates of change) would be more informative. More broadly, our findings may benefit investigators considering efforts to estimate abundance or vital rates of rare, large-river fishes in other systems. Special consideration should be given to how such estimates would be used to manage resources and whether sufficient captures and recaptures could be obtained to produce meaningful results.

ACKNOWLEDGEMENTS

This study was funded by the Upper Colorado River Endangered Fish Recovery Program. The Recovery Program is a joint effort of the U.S. Fish and Wildlife Service, U.S. Bureau of Reclamation, Western Area Power Administration, states of Colorado, Utah, and Wyoming, Upper Basin water users, environmental organizations, the Colorado River Energy Distributors Association, and the National Park Service. Funding for this research was administered by the USBR and the Department of Fish, Wildlife, and Conservation Biology and Larval Fish Laboratory (LFL) at Colorado State University. Project administration was facilitated by D. Speas, C. Morales, V. Romero, E. Thompson, J. Stahli, and T. Chart. Capture records resulted from the field sampling efforts of USFWS (Vernal, Utah, and Grand Junction, Colorado), UDWR (Vernal, Utah, and Moab, Utah), Colorado Parks and Wildlife (Grand Junction, Colorado), and LFL (Fort Collins, Colorado). Stocking data originated from Ouray National Fish Hatchery (USFWS, Vernal, Utah) and Grand Valley Endangered Fish Facility (USFWS, Grand Junction, Colorado). Maps were produced by M. Haworth. An early draft of this manuscript was reviewed and improved by K. McAbee. This is Larval Fish Laboratory Contribution 217.

REFERENCES

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petran, and F. Csaki, editors. International Symposium on Information Theory, Second edition, Budapest.
- Albrecht, B., H. Mohn, R. Kegerries, M. C. McKinstry, R. Rogers, T. Francis, B. Hines, J. Stolberg, D. Ryden, D. Elverud, B. Schliecher, K. Creighton, B. Healy, and B. Senger. 2018. Use of inflow areas in two Colorado River basin reservoirs by endangered Razorback Sucker *Xyrauchen texanus*. Western North American Naturalist 77(4):500-514.
- Anderson, C. S. 1995. Measuring and correcting for size selection in electrofishing mark-recapture experiments. Transactions of the American Fisheries Society 124(5):663-676.
- Badame, P. V., and J. M. Hudson. 2003. Reintroduction and monitoring of hatchery-reared Bonytail in the Colorado and Green rivers:1996–2001. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver.
- Barker, R. J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. Biometrics 53(2):666-677.
- Bestgen, K. R. 1990. Status review of the Razorback Sucker, *Xyrauchen texanus*. Final Report to U. S. Bureau of Reclamation, Salt Lake City, Utah, Colorado State University, Larval Fish Laboratory, Contribution 44, Fort Collins, Colorado.
- Bestgen, K. R., G. B. Haines, R. Brunson, T. Chart, M. Trammell, R. T. Muth, G. Birchell, K. Christopherson, and J. M. Bundy. 2002. Status of wild Razorback Sucker in the Green River basin, Utah and Colorado, determined from basinwide monitoring and other sampling programs. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado

River Endangered Fish Recovery Program, Denver, Colorado State University, Larval Fish Laboratory, Contribution 126, Fort Collins, Colorado

Bestgen, K. R., J. A. Hawkins, G. C. White, K. D. Christopherson, J. M. Hudson, M. H. Fuller, D. C. Kitcheyan, R. Brunson, P. Badame, G. B. Haines, J. A. Jackson, C. D. Walford, and T. A. Sorensen. 2007. Population status of Colorado Pikeminnow in the Green River basin, Utah and Colorado. *Transactions of the American Fisheries Society* 136(5):1356–1380.

Bestgen, K. R., K. A. Zelasko, R. I. Compton, and T. E. Chart. 2008. Survival, condition, habitat use, and predation of stocked Bonytail in the Green River, Colorado and Utah. *Southwestern Naturalist* 53(4):488-494.

Bestgen, K. R., K. A. Zelasko, and G. C. White. 2009. Survival of hatchery-reared Razorback Suckers *Xyrauchen texanus* stocked in the San Juan River basin, New Mexico, Colorado, and Utah. Final Report to the U.S. Fish and Wildlife Service, San Juan River Basin Recovery Implementation Program, Albuquerque, New Mexico, Colorado State University, Larval Fish Laboratory, Contribution 160, Fort Collins, Colorado.

Bestgen, K. R., J. A. Hawkins, G. C. White, C. D. Walford, P. Badame, and L. Monroe. 2010. Population status of Colorado Pikeminnow in the Green River basin, Utah and Colorado, 2006-2008. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado State University, Larval Fish Laboratory, Contribution 161, Fort Collins, Colorado

Bestgen, K. R., G. B. Haines, and A. A. Hill. 2011. Synthesis of flood plain wetland information: Timing of Razorback Sucker reproduction in the Green River, Utah, related to stream flow, water temperature, and flood plain wetland availability. Final Report to the U.S.

Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado State University, Larval Fish Laboratory, Contribution 163, Fort Collins, Colorado.

Bestgen, K. R., J. A. Hawkins, G. C. White, C. D. Walford, M. Breen, T. Jones, A. Webber, and J. Howard. 2012a. Abundance estimates for Colorado Pikeminnow in the Green River basin, Utah and Colorado. Annual report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado State University, Larval Fish Laboratory, Fort Collins, Colorado.

Bestgen, K. R., K. A. Zelasko, and G. C. White. 2012b. Monitoring reproduction, recruitment, and population status of Razorback Suckers in the upper Colorado River basin. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado State University, Larval Fish Laboratory, Contribution 170, Fort Collins, Colorado.

Bestgen, K. R., J. A. Hawkins, G. C. White, C. D. Walford, M. Breen, T. Jones, A. Webber, and J. Howard. 2013. Abundance estimates for Colorado Pikeminnow in the Green River basin, Utah and Colorado. Annual report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado State University, Larval Fish Laboratory, Fort Collins, Colorado.

Bestgen, K. R., C. D. Walford, G. C. White, J. A. Hawkins, M. T. Jones, P. A. Webber, M. Breen, J. Skorupski, J. Howard, K. Creighton, J. Logan, K. Battige, and F. B. Wright. 2018. Population status of Colorado Pikeminnow in the Green River sub-basin, Colorado and Utah, 2000–2013. Final Report to the U.S. Fish and Wildlife Service, Upper

Colorado River Endangered Fish Recovery Program, Denver, Colorado State University, Larval Fish Laboratory, Contribution 200, Fort Collins, Colorado.

Bestgen, K. R., T. E. Dowling, B. Albrecht, and K. A. Zelasko. In press. Large-river fish conservation in the Colorado River basin: progress and challenges with endangered Razorback Sucker. Pages 999-999 in D. L. Propst, J. E. Williams, K. R. Bestgen, and C. W. Hoagstrom, editors. *Standing Between Life and Extinction: Ethics and Ecology of Conserving Aquatic Species in the American Southwest*. University of Chicago Press, Chicago.

Breton, A. R., D. L. Winkelman, J. A. Hawkins, and K. R. Bestgen. 2014. Population trends of Smallmouth Bass in the upper Colorado River basin with an evaluation of removal effects. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado State University, Larval Fish Laboratory, Contribution 169, Fort Collins, Colorado.

Brown, C., and R. L. Day. 2002. The future of stock enhancements: lessons for hatchery practice from conservation biology. *Fish and Fisheries* 3(2):79-94.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173-1187.

Burdick, B. D. 2003. Monitoring and evaluating various sizes of domestic-reared Razorback Sucker stocked in the upper Colorado and Gunnison rivers: 1995-2001. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver.

- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference : a practical information-theoretic approach. Springer, New York.
- Carlson, C. A., and R. T. Muth. 1989. The Colorado River: lifeline of the American Southwest. Canadian Special Publication of Fisheries and Aquatic Sciences 106: 220–39.
- Cathcart, C. N., C. A. Pennock, C. A. Cheek, M. C. McKinstry, P. D. MacKinnon, M. M. Conner, and K. B. Gido. 2018. Waterfall formation at a desert river–reservoir delta isolates endangered fishes. *River Research and Applications* 34(8):948-956.
- Conner, M. M., S. N. Bennett, W. C. Saunders, and N. Bouwes. 2015. Comparison of tributary survival estimates of steelhead using Cormack–Jolly–Seber and Barker models: Implications for sampling efforts and designs. *Transactions of the American Fisheries Society* 144(1):34-47.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
- Dauwalter, D. C., and W. L. Fisher. 2007. Electrofishing capture probability of Smallmouth Bass in streams. *North American Journal of Fisheries Management* 27(1):162-171.
- Dowling, T. E., W. L. Minckley, P. C. Marsh, and E. S. Goldstein. 1996. Mitochondrial DNA variability in the endangered Razorback Sucker (*Xyrauchen texanus*): Analysis of hatchery stocks and implications for captive propagation. *Conservation Biology* 10(1):120–127.
- Dowling, T. E., M. J. Saltzgeber, and P. C. Marsh. 2012. Genetic structure within and among populations of the endangered Razorback Sucker (*Xyrauchen texanus*) as determined by analysis of microsatellites. *Conservation Genetics* 13(4):1073-1083.

- Durst, S. L., and T. A. Francis. 2016. Razorback sucker transbasin movement through Lake Powell, Utah. *The Southwestern Naturalist* 61(1):60-63.
- Ehlo, C. A., W. J. Goldsmith, B. R. Kesner, and P. C. Marsh. 2019. Size-specific fate and survival of June Sucker *Chasmistes liorus mictus* in Utah Lake, Utah, volume 79. BIOONE.
- Farrington, M. A., R. K. Dudley, J. L. Kennedy, S. P. Platania, and G. C. White. 2016. Colorado Pikeminnow and Razorback Sucker larval fish survey in the San Juan River during 2015. Final Report to the U.S. Fish and Wildlife Service, San Juan River Basin Recovery Implementation Program, Albuquerque, New Mexico.
- Fetherman, E. R., B. W. Avila, and D. L. Winkelman. 2014. Raft and floating radio frequency identification (RFID) antenna systems for detecting and estimating abundance of PIT-tagged fish in rivers. *North American Journal of Fisheries Management* 34(6):1065-1077.
- Flick, W. A., and D. A. Webster. 1964. Comparative first year survival and production in wild and domestic strains of Brook Trout, *Salvelinus fontinalis*. *Transactions of the American Fisheries Society* 93(1):58-69.
- Grams, P. E., and J. C. Schmidt. 2002. Streamflow regulation and multi-level flood plain formation: channel narrowing on the aggrading Green River in the eastern Uinta Mountains, Colorado and Utah. *Geomorphology* 44(3):337-360.
- Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada Geese. *Ecology* 72(2):523-533.
- Hidalgo, H. G., and J. A. Dracup. 2003. ENSO and PDO effects on hydroclimatic variations of the upper Colorado River basin. *Journal of Hydrometeorology* 4(1):5-23.

- Huggins, R. M. 1989. On the statistical analysis of capture experiments. *Biometrika* 76(1):133-140.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47(2):725-732.
- Humphrey, K. G., B. R. Kesner, and P. C. Marsh. 2016. Distribution and post-stocking survival of Bonytail in Lake Havasu, 2013 – 2016. Report to the Bureau of Reclamation, Boulder City, Nevada, Marsh & Associates, LLC, Tempe, Arizona.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76(2):297–307.
- Integrated Stocking Plan Revision Committee. 2015. Revised integrated stocking plan for Razorback Sucker and Bonytail. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver.
- Iorns, W. V., C. H. Hembree, and G. L. Oakland. 1965. Water resources of the upper Colorado River basin—Technical report. U.S. Geological Survey Professional Paper 441.
- Ireland, S. C., R. C. P. Beamesderfer, V. L. Paragamian, V. D. Wakkinen, and J. T. Siple. 2002. Success of hatchery-reared juvenile White Sturgeon (*Acipenser transmontanus*) following release in the Kootenai River, Idaho, USA. *Journal of Applied Ichthyology* 18(4-6):642–650.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration stochastic model. *Biometrika* 52:225–247.
- Justice, C., B. J. Pyper, R. C. P. Beamesderfer, V. L. Paragamian, P. J. Rust, M. D. Neufeld, and S. C. Ireland. 2009. Evidence of density- and size-dependent mortality in hatchery-reared

- juvenile White Sturgeon (*Acipenser transmontanus*) in the Kootenai River. *Canadian Journal of Fisheries & Aquatic Sciences* 66(5):802-815.
- Kegerries, R. B., B. C. Albrecht, E. I. Gilbert, W. H. Brandenburg, A. L. Barkalow, M. C. McKinstry, H. E. Mohn, B. D. Healy, J. R. Stolberg, E. C. O. Smith, C. B. Nelson, and R. J. Rogers. 2017. Occurrence and reproduction by Razorback Sucker (*Xyrauchen texanus*) in the Grand Canyon, Arizona. *The Southwestern Naturalist*:227-232.
- Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. *Biometrics* 51(1):293-308.
- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollack's robust design. *Ecology* 78(2):563-578.
- Kendall, W. L. 1999. Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology* 80(8):2517-2525.
- Kesner, B. R., C. A. Ehlo, J. B. Wisenall, and P. C. Marsh. 2017. Comparative survival of repatriated Razorback Suckers in Lower Colorado River Reach 3, 2014–2016. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada, Marsh & Associates, LLC, Tempe, Arizona.
- Korman, J., M. Yard, C. Walters, and L. G. Coggins. 2009. Effects of fish size, habitat, flow, and density on capture probabilities of age-0 Rainbow Trout estimated from electrofishing at discrete sites in a large river. *Transactions of the American Fisheries Society* 138(1):58-75.
- LaGory, K., T. Chart, K. Bestgen, J. Wilhite, S. Capron, D. Speas, H. Hermansen, K. McAbee, J. Mohrman, M. Trammell, and B. Albrecht. 2012. Study plan to examine the effects of

- using larval Razorback Sucker occurrence in the Green River as a trigger for Flaming Gorge Dam peak releases. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver.
- LaGory, K., K. Bestgen, H. Patno, J. Wilhite, D. Speas, and M. Trammell. In review. Evaluation and suggested revisions of flow and temperature regulations for endangered fish in the Green River downstream of Flaming Gorge Dam. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver.
- Lanigan, S. H., and H. M. Tyus. 1989. Population size and status of the Razorback Sucker in the Green River basin, Utah and Colorado. *North American Journal of Fisheries Management* 9(1):68-73.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62(1):67–118.
- Marsh, P. C., B. R. Kesner, and C. A. Pacey. 2005. Repatriation as a management strategy to conserve a critically imperiled fish species. *North American Journal of Fisheries Management* 25(2):547–556.
- Marsh, P. C., T. E. Dowling, B. R. Kesner, T. F. Turner, and W. L. Minckley. 2015. Conservation to stem imminent extinction: The fight to save Razorback Sucker *Xyrauchen texanus* in Lake Mohave and its implications for species recovery. *Copeia* 103(1):141-156.
- Martinez, P. J., and A. L. Kolz. 2016. Recommended electrofishing guidelines for upper Colorado River basin habitats containing endangered fishes. Final Report to the U.S.

- Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver.
- McAda, C. W., and R. S. Wydoski. 1980. The Razorback Sucker, *Xyrauchen texanus*, in the upper Colorado River basin, 1974–76. U. S. Fish and Wildlife Service Technical Papers 99.
- Miller, R. B. 1954. Comparative survival of wild and hatchery-reared Cutthroat Trout in a stream. *Transactions of the American Fisheries Society* 83(1):120–130.
- Minckley, W. L. 1983. Status of the Razorback Sucker, *Xyrauchen texanus* (Abbott), in the Lower Colorado River basin. *The Southwestern Naturalist* 28(2):23.
- Minckley, W. L., P. C. Marsh, J. E. Brooks, J. E. Johnson, and B. L. Jensen. 1991. Management toward recovery of the Razorback Sucker. Pages 303–357 in W. L. Minckley, and J. E. Deacon, editors. *Battle Against Extinction: Native Fish Management in the American West*. The University of Arizona Press, Tucson.
- Modde, T., K. P. Burnham, and E. J. Wick. 1996. Population status of the Razorback Sucker in the middle Green River (USA). *Conservation Biology* 10(1):110–119.
- Modde, T., Z. H. Bowen, and D. C. Kitcheyan. 2005. Spatial and temporal use of a spawning site in the Middle Green River by wild and hatchery-reared Razorback Suckers. *Transactions of the American Fisheries Society* 134(4):937–944.
- Muth, R. T., and J. B. Ruppert. 1996. Effects of two electrofishing currents on captive ripe Razorback Suckers and subsequent egg-hatching success. *North American Journal of Fisheries Management* 16:473–476.
- Muth, R. T., L. W. Crist, K. E. LaGory, J. W. Hayse, K. R. Bestgen, T. P. Ryan, J. K. Lyons, and R. A. Valdez. 2000. Flow and temperature recommendations for endangered fishes in the

- Green River downstream of Flaming Gorge Dam. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver.
- Nesler, T. P., K. Christopherson, J. M. Hudson, C. W. McAda, F. Pfeifer, and T. E. Czapla. 2003. An integrated stocking plan for Razorback Sucker, Bonytail, and Colorado Pikeminnow for the Upper Colorado River Endangered Fish Recovery Program. Addendum to State Stocking Plans, U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver.
- Olden, J. D., N. L. Poff, and K. R. Bestgen. 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecological Monographs* 76(1):25-40.
- Olla, B. L., M. W. Davis, and C. H. Ryer. 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. *Bulletin of Marine Science* 62(2):531–550.
- Osmundson, D. B., and S. C. Seal. 2009. Successful spawning by Razorback Sucker in the Gunnison and Colorado rivers, as evidenced by larval fish collections, 2002-2007. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver.
- Pinter, K., S. Weiss, E. Lautsch, and G. Unfer. 2017. Survival and growth of hatchery and wild Brown Trout (*Salmo trutta*) parr in three Austrian headwater streams. *Ecology of Freshwater Fish*:n/a-n/a.
- Pitman, V. M., and S. Gutreuter. 1993. Initial poststocking survival of hatchery-reared fishes. *North American Journal of Fisheries Management* 13(1):151–159.

- Platania, S. P., K. R. Bestgen, M. M. Moretti, J. E. Brooks, and D. L. Propst. 1991. Status of Colorado Squawfish and Razorback Sucker in the San Juan River, Colorado, New Mexico, and Utah. *Southwestern Naturalist* 36(1):147–150.
- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *The Journal of Wildlife Management* 46(3):752-757.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107. 97 pp.
- Schooley, J. D., B. R. Kesner, J. R. Campbell, J. M. Barkstedt, and P. M. Marsh. 2008. Survival of Razorback Sucker in the lower Colorado River. Final Report, Agreement Number 06-FC-30-0002, Arizona State University, Tempe.
- Seber, G. A. 1965. A note on the multiple recapture census. *Biometrika* 52:249–259.
- Seber, G. A. F. 1986. A review of estimating animal abundance. *Biometrics* 42(2):267-292.
- Shaughnessy, M. 2010. Operation and maintenance of Ouray National Fish Hatchery. Annual report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver.
- Stahl, T. P., G. P. Thiede, R. A. Stein, E. M. Lewis, M. R. Austin, and D. A. Culver. 1996. Factors affecting survival of age-0 saugeye *Stizostedion vitreum* x *S. canadense* stocked in Ohio reservoirs. *North American Journal of Fisheries Management* 16(2):378–387.
- Stout, J. B., M. M. Conner, P. Budy, P. D. Mackinnon, and M. C. McKinstry. 2019. We ain't afraid of no ghosts: Tracking habitat interactions and movement dynamics of ghost tags under differing flow conditions in a sand-bed river. *North American Journal of Fisheries Management* 39(6):1337-1347.

- STReaMS. 2020. Species Tagging, Research and Monitoring System: A Centralized Database for the Upper Colorado and San Juan River Endangered Fish Recovery Programs. Accessed via the internet at <https://streamsystem.org>.
- Suboski, M. D., and J. J. Templeton. 1989. Life skills training for hatchery fish: Social learning and survival. *Fisheries Research* 7(4):343–352.
- Sugiura, N. 1978. Further analysts of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics - Theory and Methods* 7(1):13 – 26.
- Tyus, H. M. 1987. Distribution, reproduction, and habitat use of the Razorback Sucker in the Green River, Utah, 1979–1986. *Transactions of the American Fisheries Society* 116(1):111–116.
- U.S. Bureau of Reclamation. 2006. Record of Decision, Operation of Flaming Gorge Dam, Final Environmental Impact Statement.
- U.S. Fish and Wildlife Service. 2002. Razorback Sucker (*Xyrauchen texanus*) Recovery Goals: amendment and supplement to the Razorback Sucker Recovery Plan. U.S. Fish and Wildlife Service, Mountain-Prairie Region (6), Denver.
- U.S. Fish and Wildlife Service. 2018a. Species status assessment report for the Razorback Sucker *Xyrauchen texanus*. U.S. Fish and Wildlife Service, Mountain-Prairie Region (6), Denver.
- U.S. Fish and Wildlife Service. 2018b. Razorback Sucker (*Xyrauchen texanus*) 5-Year Review: Summary and Evaluation. U.S. Fish and Wildlife Service, Mountain-Prairie Region (6), Denver.

- Upper Colorado River Basin Environmental Impact Statement Project. 1948. Upper Colorado River basin compact: entered into by the states of Arizona, Colorado, New Mexico, Utah, Wyoming. Santa Fe, New Mexico.
- Van Steeter, M. M., and J. Pitlick. 1998. Geomorphology and endangered fish habitats of the upper Colorado River, 1, Historic changes in streamflow, sediment load, and channel morphology. *Water Resources Research* 34(2):287–302.
- Webber, P. A., and D. Beers. 2014. Detecting Razorback Suckers using passive integrated transponder tag antennas in the Green River, Utah. *Journal of Fish and Wildlife Management* 5(1):191-196.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 Supplement:120–138.
- Zelasko, K. A. 2008. Survival rate estimation and movement of hatchery-reared Razorback Suckers *Xyrauchen texanus* in the upper Colorado River basin, Utah and Colorado. Master's thesis. Colorado State University, Fort Collins.
- Zelasko, K. A., K. R. Bestgen, and G. C. White. 2009. Survival rate estimation and movement of hatchery-reared Razorback Suckers *Xyrauchen texanus* in the upper Colorado River basin, Utah and Colorado. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado State University, Larval Fish Laboratory, Contribution 159, Fort Collins, Colorado.
- Zelasko, K. A., K. R. Bestgen, and G. C. White. 2010. Survival rates and movement of hatchery-reared Razorback Suckers in the upper Colorado River basin, Utah and Colorado. *Transactions of the American Fisheries Society* 139(5):1478-1499.

- Zelasko, K. A., K. R. Bestgen, and G. C. White. 2011. Survival rate estimation of hatchery-reared Razorback Suckers *Xyrauchen texanus* stocked in the upper Colorado River basin, Utah and Colorado, 2004–2007. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado State University, Larval Fish Laboratory, Contribution 162, Fort Collins, Colorado.
- Zelasko, K. A., K. R. Bestgen, J. A. Hawkins, and G. C. White. 2016. Evaluation of a long-term predator removal program: Abundance and population dynamics of invasive Northern Pike in the Yampa River, Colorado. *Transactions of the American Fisheries Society* 145:1153-1170.
- Zelasko, K. A., K. R. Bestgen, and G. C. White. 2018. Abundance and survival rates of Razorback Suckers *Xyrauchen texanus* in the Green River, Utah, 2011–2013. Final Report to the U.S. Fish and Wildlife Service, Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado State University, Larval Fish Laboratory, Contribution 203, Fort Collins, Colorado.

Table 1. Razorback Sucker captures ($n = 4,145$) by reach, year, and pass in the Green River, Utah, 2011–2013. See Figure 1 for reach definitions.

Reach	Pass			Total
	1	2	3	
2011				
Middle Green	28	111	72	211
Desolation-Gray	118	146	156	420
Lower Green	323	301	309	933
Total	469	558	537	1,564
2012				
Middle Green	69	32	32	133
Desolation-Gray	146	428	142	716
Lower Green	242	243	175	660
Total	457	703	349	1,509
2013				
Middle Green	30	114	183	327
Desolation-Gray	121	202	146	469
Lower Green	48	77	151	276
Total	199	393	480	1,072

Table 2. Razorback Suckers stocked annually and year of stocking for all individuals ($n = 3,932$) initially captured during this study in three reaches of the Green River, Utah, 2011–2013. See Figure 1 for reach definitions.

Year of stocking	Middle Green					Desolation-Gray					Lower Green					Total		
	Stocked		Captured, %			Stocked		Captured, %			Stocked		Captured, %			Stocked		Captured
	<i>n</i>	%	2011	2012	2013	<i>n</i>	%	2011	2012	2013	<i>n</i>	%	2011	2012	2013	<i>n</i>	%	%
1995	905	0.9														905	0.5	
1996	1,067	1.1														1067	0.6	
1997																		
1998	389	0.4	0.5													389	0.2	<0.1
1999	1,357	1.4	1.4													1357	0.8	0.1
2000	224	0.2	1.4	0.8	0.3											224	0.1	0.1
2001																		
2002													0.1			274 ^a	0.2	<0.1
2003	8,492	8.6	7.1	4.5	2.2			0.4	0.5		2,376	3.0	0.6	0.5	0.8	10,868	6.1	1.1
2004	9,621	9.7	5.7	3.8	2.6			1.7	0.6		5,955	7.6	2.5	3.8	2.3	15,576	8.8	2.2
2005	4,864	4.9	6.7	1.5	1.3			1.0	0.6	0.5	4,231	5.4	1.8	2.2	0.8	9,095	5.1	1.6
2006	10,079	10.2	1.4	2.3	1.0			0.7	0.1		10,133	12.9	2.7	3.3		20,212	11.4	1.4
2007	7,748	7.8	5.2	4.5	3.5			7.3	2.8	0.9	8,538	10.9	3.5	2.8	2.3	16,286	9.2	3.4
2008	8,387	8.5	17.6	11.4	12.1			15.3	14.6	7.1	10,161	12.9	21.5	19.7	8.9	18,548	10.4	15.6
2009	14,269	14.4	37.1	37.9	28.1			32.6	19.7	14.9	5,013	6.4	26.6	21.4	13.5	19,282	10.8	24.1
2010	11,404	11.5	15.7	12.9	25.9			41.4	34.2	26.8	10,024	12.7	40.7	18.9	6.6	21,428	12.1	29.1
2011	9,089	9.2		20.5	12.1				27.1	16.7	12,028	15.3		27.4	21.2	21,117	11.9	13.8
2012	10,912	11.0			10.9					32.7	10,194	13.0			43.6	21,106	11.9	7.4
Total	98,807	100.0	100.0	100.0	100.0			100.0	100.0	100.0	78,653	100.0	100.0	100.0	100.0	177,734 ^b	100.0	100.0

^a Stocking data for these fish contained no location information.

^b Reach totals sum to 177,460, due to 274 fish stocked during 2002 with no location information.

Table 3. Robust design multi-state models to estimate survival rate (S), capture probability (p), transition rate (ψ), and abundance (derived from Huggins model parameters) for Razorback Suckers in three reaches of the Green River, 2011–2013. AIC_c = Akaike’s Information Criterion, adjusted for small sample size bias; Delta AIC_c = AIC_c – minimum AIC_c ; AIC_c Weight = ratio of delta AIC_c relative to entire set of candidate models; Model Likelihood = ratio of AIC_c weight relative to AIC_c weight of best model; K = number of parameters; Deviance = log-likelihood of the model – log-likelihood of the saturated model. Year = study interval (S) or study year (p); AtLarge = time between stocking and initial capture of the study (< 1 year, > 1 year); stkTL = total length at time of stocking; stkYR = year of stocking. See Figure 1 for reach definitions.

Model			Delta AIC_c	AIC_c weights	Model likelihood	K	Deviance
$S(\text{reach*year+AtLarge})$	$\psi(\text{reach})$	$p(\text{reach*year*pass})$	0	0.512	1.000	40	10372.590
$S(\text{reach*year})$	$\psi(\text{reach})$	$p(\text{reach*year*pass})$	2.9337	0.118	0.231	39	10377.563
$S(\text{reach*year+AtLarge})$	$\psi(\text{reach})$	$p(\text{reach*year*pass+stkTL}^2)$	3.5337	0.087	0.171	42	10372.042
$S(\text{reach*year})$	$\psi(\text{reach})$	$p(\text{reach*year*pass+stkTL}^2)$	3.9024	0.073	0.142	41	10374.452
$S(\text{reach*year+stkTL})$	$\psi(\text{reach})$	$p(\text{reach*year*pass})$	4.2061	0.062	0.122	40	10376.796
$S(\text{reach*year})$	$\psi(\text{reach})$	$p(\text{reach*year*pass+stkTL})$	4.2380	0.061	0.120	40	10376.828
$S(\text{reach*year+stkTL}^2)$	$\psi(\text{reach})$	$p(\text{reach*year*pass})$	4.7054	0.049	0.095	41	10375.255
$S(\text{reach*year})$	$\psi(\text{reach})$	$p(\text{reach*year*pass+stkTL}^3)$	5.2577	0.037	0.072	42	10373.766
$S(\text{reach*year+stkYR})$	$\psi(\text{reach})$	$p(\text{reach*year*pass})$	13.3704	0.001	0.001	54	10357.305

Table 4. Recaptures of Razorback Suckers initially captured in three reaches of the Green River, Utah, 2011–2013. Column “Released” includes fish initially captured and released each year, plus fish recaptured and released that same year (e.g., Middle Green reach, 2013: 323 = 313 initially captured, plus 7 initially captured in 2011 and recaptured in 2013, plus 3 initially captured in 2012 and recaptured in 2013). See Figure 1 for reach definitions.

Initial capture year	Released	Recapture year		
		2011	2012	2013
Middle Green				
2011	210	1		7
2012	132		1	3
2013	323			4
Desolation-Gray				
2011	411	9	17	7
2012	704		12	16
2013	460			8
Lower Green				
2011	884	45	44	10
2012	643		17	6
2013	275			1

Table 5. Razorback Sucker abundance estimates (\hat{N}), 95% confidence intervals (CI), and coefficients of variation (CV) in three reaches of the Green River, Utah, during two study periods, 2006–2008 (Bestgen et al. 2012b) and 2011–2013. See Figure 1 for reach definitions.

Reach	Year	<i>N</i>	95% CI		CV (%)	Year	<i>N</i>	95% CI		CV (%)
			Lower	Upper				Lower	Upper	
Middle Green	2006	576	227	1,608	55	2011	13,102	2,705	66,817	99
	2007	3,146	1,039	9,764	63	2012	14,453	4,203	50,521	71
	2008	1,218	448	3,514	57	2013	8,717	3,692	21,253	47
Desolation-Gray	2006	474	207	1,217	49	2011	6,412	3,516	12,006	32
	2007	3,011	772	12,076	81	2012	11,448	7,470	17,765	22
	2008	836	280	2,677	64	2013	8,014	4,447	14,772	32
Lower Green	2006	1,582	1,061	2,446	22	2011	5,791	4,501	7,541	13
	2007	5,153	2,588	10,460	37	2012	10,808	8,063	14,566	15
	2008	2,597	1,595	4,359	26	2013	16,554	5,916	47,233	57

Table 6. Projected declining abundance trends of Razorback Suckers in the Green River subbasin in the absence of recruitment—the present condition—if stocking were to cease upon expiration of the Upper Colorado River Endangered Fish Recovery Program multi-stakeholder cooperative agreement in 2023. Starting abundance of 30,000 approximates the 2013 Green River Razorback Sucker abundance estimate (U.S. Fish and Wildlife Service 2018) and 6,000 stocked fish with mean size 350 mm TL (Integrated Stocking Plan Revision Committee 2015) are added annually until 2023. Assumed survival rate estimates of 0.40 for the first year and 0.75 thereafter were from Zelasko et al. (2010).

		Year						
	2020	2021	2022	2023	2024	2025	2026	2027
30,000	30,000	22,500	16,875	12,656	9,492	7,119	5,339	4,005
6,000	6,000	2,400	1,800	1,350	1,013	759	570	427
		6,000	2,400	1,800	1,350	1,013	759	570
			6,000	2,400	1,800	1,350	1,013	759
36,000	36,000	30,900	27,075	18,206	13,655	10,241	7,681	5,761

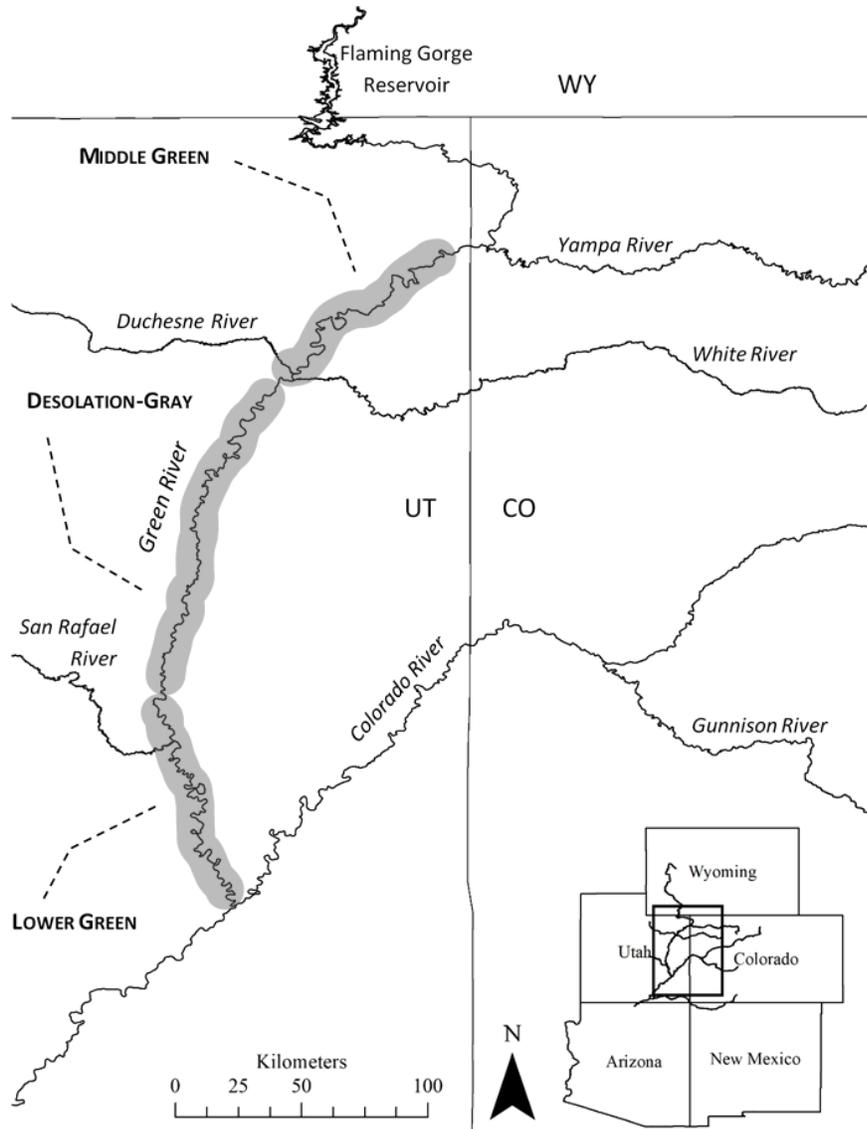


Figure 1. Map of the upper Colorado River basin, including three study reaches of the Green River, Utah. Middle Green = Green River from the mouth of Whirlpool Canyon downstream to near the White River confluence (river kilometer [RKM] 539.4–396.0 [measuring from its confluence with the Colorado River], excluding Split Mountain Canyon), Desolation-Gray = Green River from the White River confluence downstream to near Green River, Utah, including Desolation and Gray canyons (RKM 395.9–206.1), and Lower Green = Green River from Green River, Utah, downstream to the Colorado River confluence (RKM 193.2–0.0).

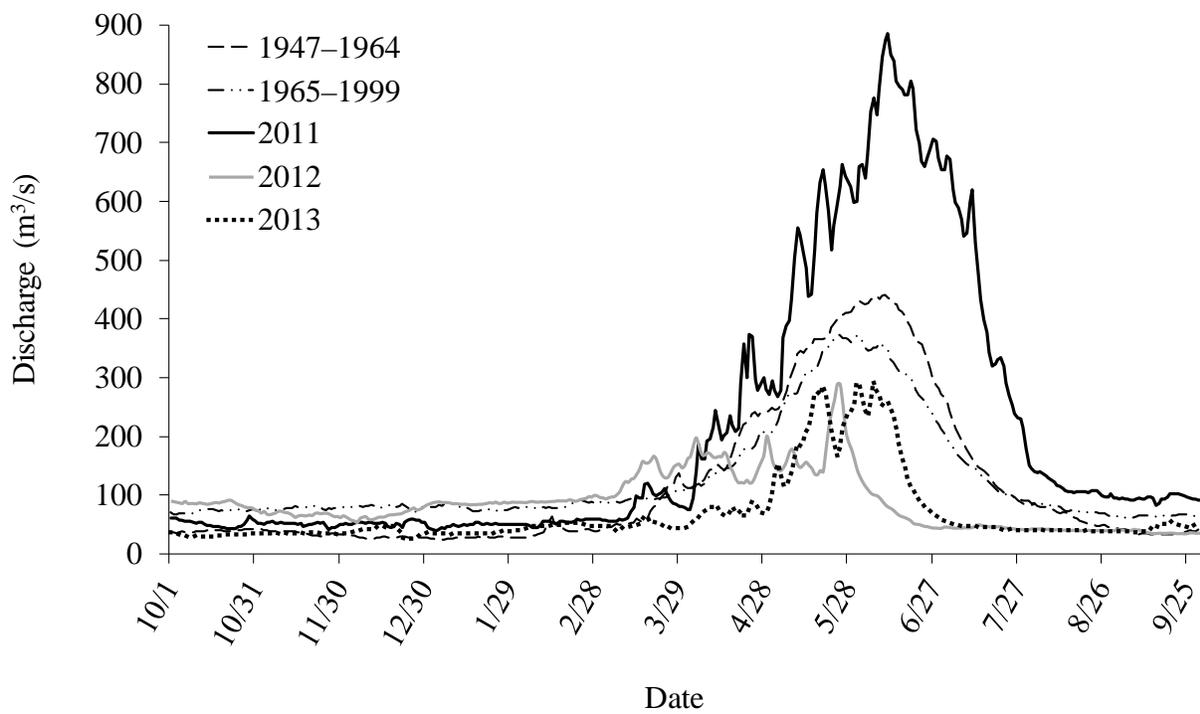


Figure 2. Mean daily discharge of the Green River near Jensen, Utah (U.S. Geological Survey gage 09261000), for water years 1947–1964 (pre-impoundment of Flaming Gorge dam), 1965–1999 (post-impoundment), and study years 2011, 2012, and 2013.

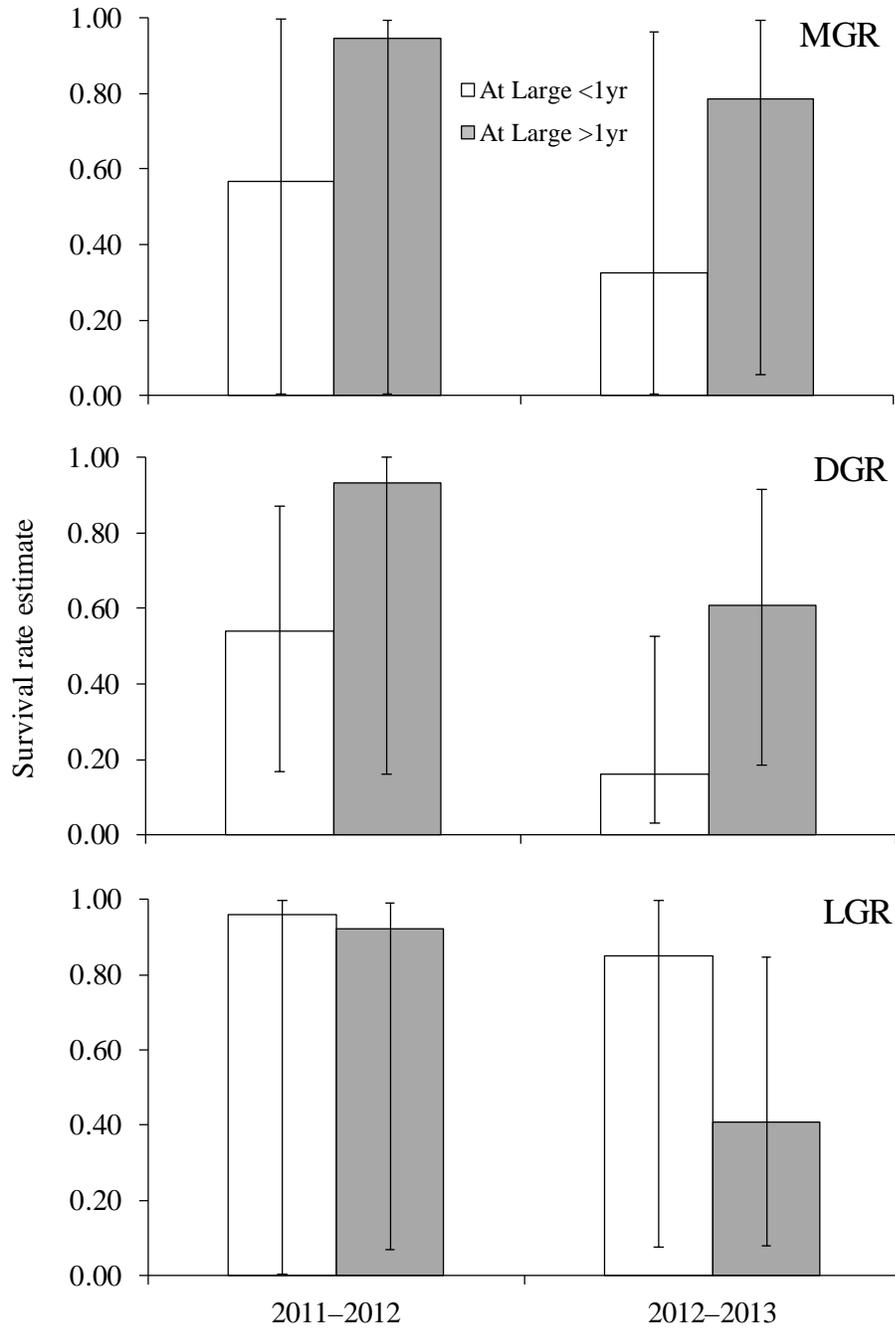


Figure 3. Survival rate estimates and 95% confidence intervals (vertical bars) by interval and time at large from stocking to initial capture during this study for Razorback suckers in three reaches of the Green River, Utah, 2011–2013. MGR = Middle Green, DGR = Desolation-Gray, LGR = Lower Green. See Figure 1 for reach definitions.

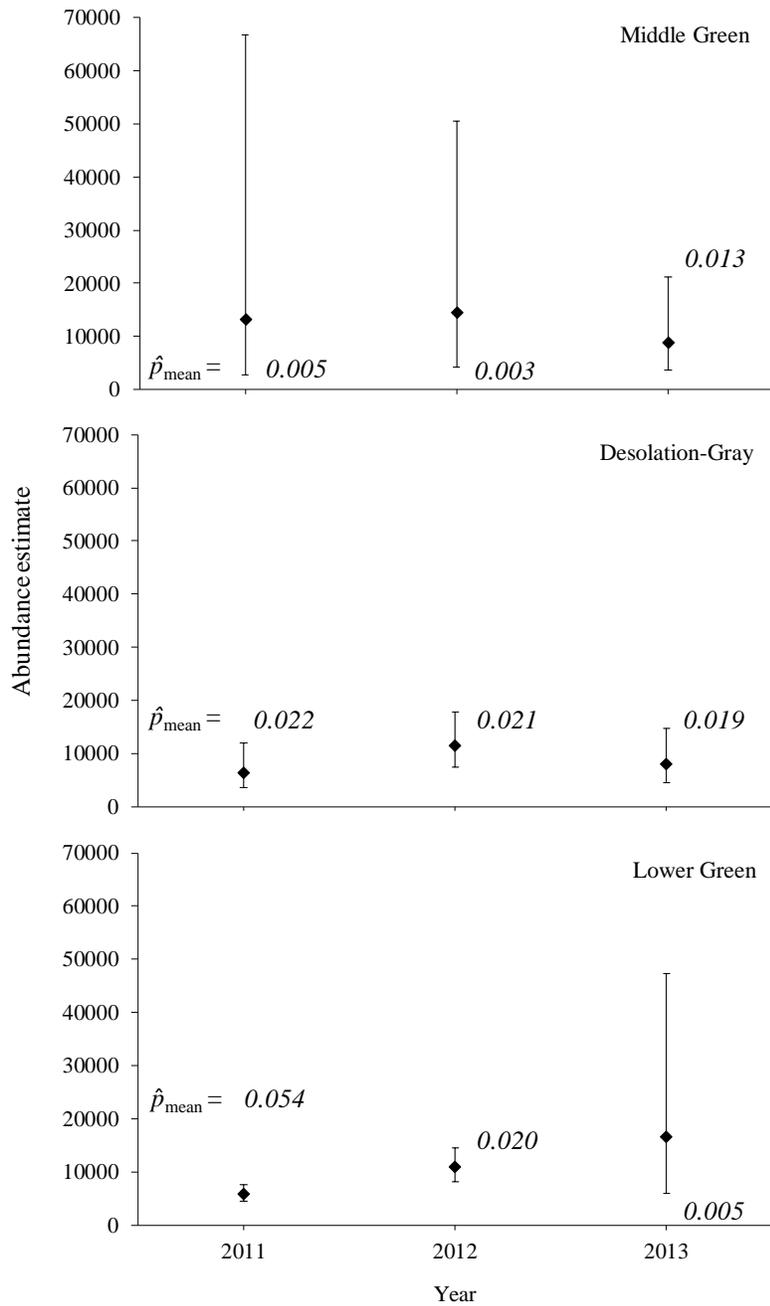


Figure 4. Abundance estimates, 95% confidence intervals (vertical bars), and associated mean annual capture probability estimates (\hat{p}_{mean} , average of sampling passes) for Razorback suckers captured in three reaches of the Green River, Utah, 2011–2013. See Figure 1 for reach definitions.

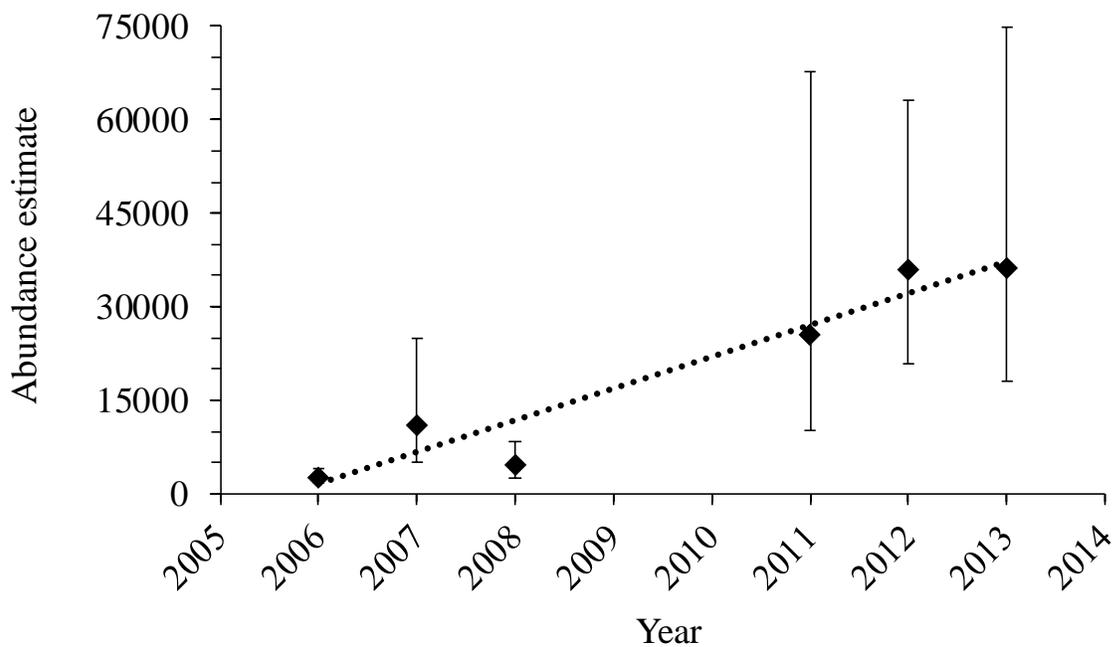


Figure 5. Model-averaged abundance estimates, 95% confidence intervals (vertical bars), and linear trend line (dotted line; $R^2 = 0.92$) for Razorback suckers captured in the Green River, Utah, 2006–2008 and 2011–2013. Estimates are for Middle Green, Desolation-Gray, and Lower Green reaches combined and may differ slightly from sums of reach-specific estimates calculated without model averaging in this report and Bestgen et al. (2012b). See Figure 1 for reach definitions.

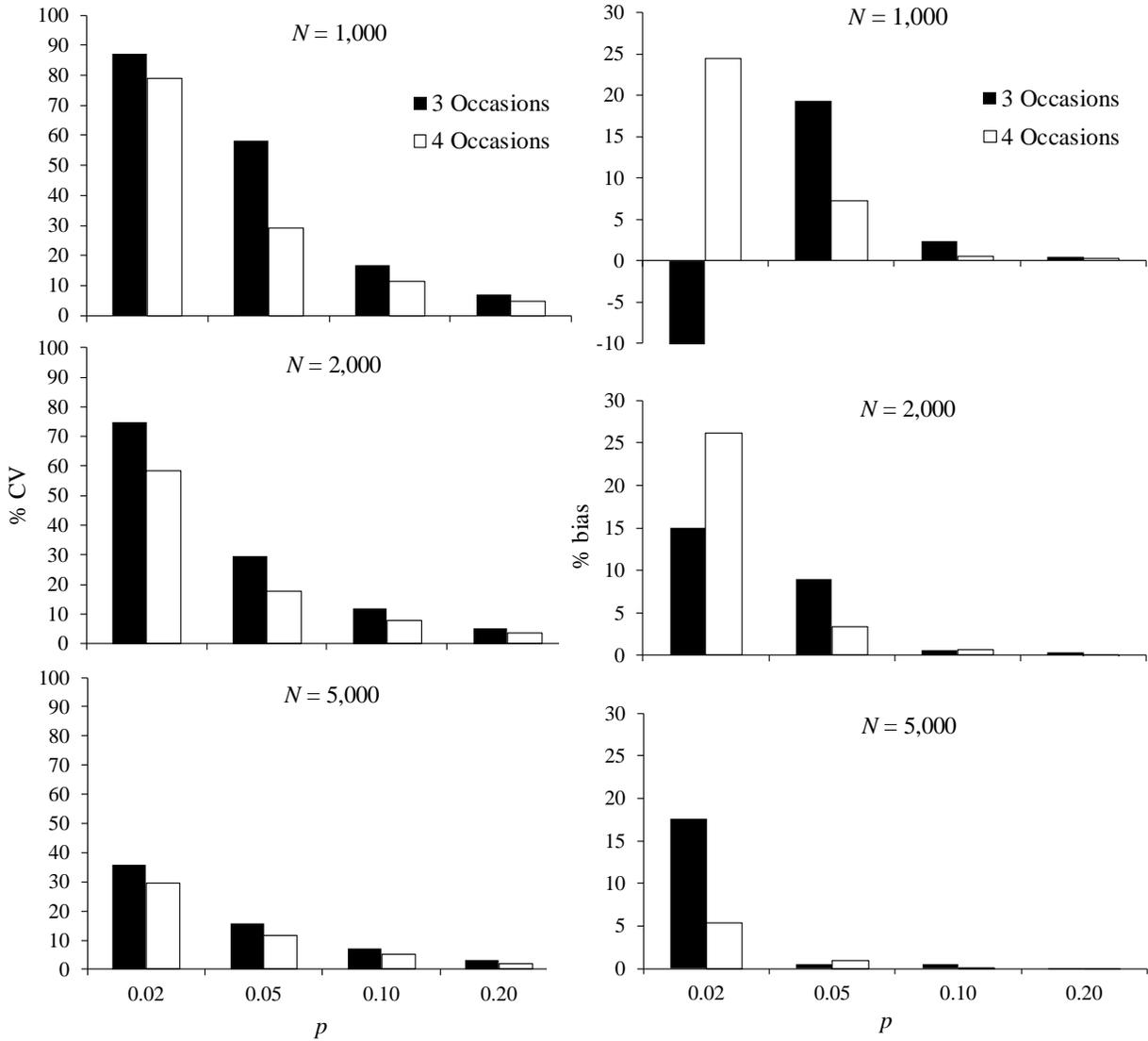


Figure 6. Simulation results that depict precision (coefficient of variation, CV) and bias of abundance estimates for three true population sizes of fish (N), under four probabilities of capture per pass (p), using three or four sampling occasions. We conducted 1,000 simulations per combination, except $p = 0.02$ (100 simulations) which produced convergence errors or non-intuitive results (e.g., estimated population size ≥ 10 times higher than true population size or lower bias for fewer occasions). Adapted from Bestgen et al. (2012b).