Abundance and survival rates of razorback suckers *Xyrauchen texanus* in the Green River, Utah, 2011–2013

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EXECUTIVE SUMMARY

Quantified demographic rates are useful for evaluating status and trajectory of an animal population. Endangered species management, in particular, often relies on such quantifiable population descriptors to guide the recovery process. The most recent Recovery Goals (2002) for federally endangered razorback sucker *Xyrauchen texanus* (Abbott), family Catostomidae, require that two "genetically and demographically viable, self-sustaining" adult populations, each exceeding 5,800 individuals, exist in the Upper Colorado River Basin (UCRB) before downlisting or delisting can occur. Between 1995 and 2012, nearly 178,000 razorback suckers were stocked into the Green River basin to help achieve that abundance target. While no monitoring effort exists specifically for adult razorback sucker populations, studies to evaluate the survival of stocked individuals concluded that stocking larger individuals in seasons other than summer should improve the very low first-year survival of hatchery-reared razorback suckers. A separate study assessed the ability to estimate razorback sucker abundance using data collected during Colorado pikeminnow *Ptychocheilus lucius* abundance estimation sampling and concluded that recaptures were insufficient during the 2006–2008 period to produce useful parameter estimates. In more recent years, captures of razorback suckers during sampling for various projects within the UCRB have increased. Thus, this study was conducted to determine if the increased encounters of razorback suckers during Colorado pikeminnow abundance estimation sampling in 2011–2013 produced sufficient mark-recapture data to estimate reliable survival and transition rates, capture probabilities, and abundance estimates for razorback suckers in the Green River basin.

The study area encompassed three reaches: Green River from the mouth of Whirlpool Canyon downstream to near the White River confluence ("Middle Green River", RK 539.4–396.0 [RM 334.0–246.0], excluding Split Mountain Canyon); Green River from the White River confluence downstream to near Green River, Utah, including Desolation and Gray canyons ("Desolation-Gray", RK 395.9–206.1 [RM 245.9–128.0]); and Green River from Green River, Utah, downstream to the Colorado River confluence ("Lower Green River", RK 193.2–0 [RM 120.0–0]; Figure 1). A minimum of three electrofishing passes were attempted, and razorback suckers were scanned for the presence of a PIT tag and tagged, when necessary. Data were analyzed using closed, robust design, multi-state models.

The final dataset for parameter estimation consisted of 4,145 capture events of 3,932 unique razorback suckers, only 5.3% of which were captured more than once during the study period. The few recaptures of razorback suckers resulted in very low capture probability estimates and imprecise estimates of abundance, survival rates, and transition rates. Capture probabilities (mean: 0.02, range:

0.002–0.056) were lower than those of Colorado pikeminnow during the same sampling effort, which were also the lowest recorded since Green River abundance estimation sampling began in year 2000. Abundance estimates increased from 2006-2008 to 2011-2013, likely a product of continued or increased stocking through time, and were highest but least precise in upstream Middle Green River reach and declined downstream. Annual abundance varied greatly, and the level of abundance change estimated between years is not likely for relatively large and longer-lived fish, such as razorback sucker. Instead, low capture rates and estimate bias or imprecision are likely factors affecting highly variable estimates among years. A significant factor affecting survival rate estimates was time at large from stocking to first capture during this study, with higher survival for those at large > 1 year in Middle Green River and Desolation-Gray reaches. The effect corresponded to the "first year in the river" effect in our previous studies of stocked razorback sucker survival, which showed that fish stocked more recently had lower survival rates. Total length at capture or at stocking was not an influential effect for estimating razorback sucker survival or capture probability, contrary to our previous survival analyses, likely due to increased size uniformity. Meaningful transition rate estimates were precluded by too few observations of among-year movements between reaches. However, most of those few movements (and highest transition rates) were out of Desolation-Gray reach and most movement was upstream, contrary to previous and more robust movement analyses for hatchery-reared razorback suckers. All parameter estimates for Lower Green River reach in 2013 were compromised by low probabilities of capture due to reverse polarization of electrofishing equipment.

Ultimately, recaptures of razorback suckers during Colorado pikeminnow abundance estimation sampling in the Green River basin were inadequate to produce precise population parameter estimates. The razorback sucker population in the UCRB consists almost entirely of hatchery-reared individuals, so survival analyses may be sufficient to describe dynamics at present. However, studies in the UCRB have documented successful spawning by those stocked fish, as well as survival to the juvenile life stage of wild-produced larvae entrained into floodplain wetlands with the aid of experimental flows from Flaming Gorge Dam. 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. We recommend:

- Investigating ways to increase razorback sucker capture probabilities, such as: increasing sampling efforts for the species, sampling concentration areas more completely, and employing additional data from other subbasins, tributaries, projects, and gear (e.g., portable or fixed PIT tag scanning antennas already in place throughout the Upper Colorado River Basin).

- Investigating reasons for continued lower initial post-stocking survival of razorback suckers (e.g., fish condition, predator naïveté, and lack of flow acclimation).
- Collecting razorback sucker length and weight data before fish are stocked if inclusion of condition indices is desired in future analyses.
- Continuing to collect razorback sucker data from the White River and other tributaries and incorporate in future parameter estimation, when possible, to elucidate the role of tributaries in Upper Colorado River Basin population dynamics.
- Analyzing razorback sucker encounter data (including other studies and PIT tag scanning antennas) at a finer scale and over longer periods and larger areas to more accurately depict the species' survival and movement patterns.
- Incorporating results of this study and future analyses into a razorback sucker monitoring program, which includes early life stages as well as adults.

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KEY WORDS

Upper Colorado River Basin, demographic parameters, endangered fishes, recovery, stocking

INTRODUCTION

Demographic parameters that describe population size as well as birth, movement, and mortality rates are useful to ecologists attempting to understand the fundamental basis for population change and to managers attempting to maintain or enhance abundance of imperiled animal populations in need of conservation. In fact, section 4 of the Endangered Species Act of 1973 (as amended), requires that recovery plans for endangered species include "objective and measurable criteria" to determine when a species can be removed from the list. Although not required, demographic parameters such as population abundance or population growth rate are often used as part of these criteria.

The highly modified Colorado River (Iorns et al. 1965; Van Steeter and Pitlick 1998) of the American Southwest desert supports several endangered species that are currently the focus of recovery efforts. One of these species, razorback sucker *Xyrauchen texanus,* has experienced dramatic declines in distribution and abundance resulting largely from anthropogenic modifications to aquatic habitats (Minckley et al. 1991). Natural, self-sustaining populations of the species are now rare (Bestgen et al. In review). Efforts to recover razorback sucker involve several management actions, including stocking hatchery-reared individuals, protecting and connecting critical habitat, managing nonnative species, restoring more natural flow and temperature regimes, and monitoring populations (http://www.coloradoriverrecovery.org/general-information/the-fish/razorback-sucker.html). Increased encounters (Bestgen et al. 2012a; Bestgen et al. 2013), movement among subbasins (Durst and Francis 2016), apparent range expansion (Webber et al. 2013), and documented larval survival to the juvenile life stage (Albrecht et al. 2010; Skorupski et al. 2013; Albrecht et al. 2014; Schelly et al. 2014; Schelly and Breen 2015; Schelly et al. 2016; Albrecht et al. In press) strengthened interest in understanding abundance of razorback sucker in the Green River basin.   While no dedicated razorback sucker monitoring program exists in the Upper Colorado River Basin (UCRB), survival estimates for stocked individuals have been quantified using mark-recapture data obtained from other sampling (Zelasko et al. 2009; Zelasko et al. 2011) and requirements for a successful monitoring plan were detailed by Bestgen et al. (2012b). This study was undertaken to determine if data collected during Colorado pikeminnow *Ptychocheilus lucius* abundance estimation sampling was adequate to effectively monitor populations of razorback sucker. We used mark-recapture data collected during Colorado pikeminnow abundance sampling, 2011–2013, to estimate survival rates, transition rates, capture probabilities, and abundance estimates for razorback suckers in the Green River.

Distribution and status

Razorback sucker is a catostomid endemic to the Colorado River Basin (Minckley et al. 1991). Early observers documented widespread distribution from Mexico to Wyoming, but the species is now rare (Minckley 1983; Minckley et al. 1991; Platania et al. 1991; Modde et al. 1996; Bestgen et al. 2002; Marsh et al. 2003; Marsh et al. 2015; Bestgen et al. In review). Decline of razorback sucker coincided with dam construction and other habitat alterations as well as introduction of non-native species, leaving only small, fragmented populations. For example, between 1980 and 2000 in the UCRB, once widely-distributed razorback suckers were captured only sporadically in the Colorado, Green, Yampa, and San Juan rivers, Utah, Colorado, and New Mexico; the largest population of several hundred individuals was concentrated in the middle portion of the Green River, between the Duchesne and Yampa rivers (Bestgen 1990; Minckley et al. 1991). However, wild fish have since been extirpated throughout the UCRB (Bestgen 1990; Bestgen et al. 2002; Bestgen et al. In review). In the lower Colorado River basin downstream of Glen Canyon Dam, populations are found primarily in lakes Mohave, Mead, and Havasu, Arizona and Nevada (Marsh et al. 2003; Albrecht et al. 2008). The once large, wild population in Lake Mohave is effectively extirpated and most lower Colorado River basin populations are maintained by stocking cultured individuals (Wisenall et al. 2015; Bestgen et al. In review). Few juvenile razorback suckers had been encountered anywhere in the Colorado River Basin (McAda and Wydoski 1980; Gutermuth et al. 1994; Bestgen et al. 2002; Marsh et al. 2005) and recruitment failure is thought to be the primary reason for decline of the species throughout its range (Minckley 1983; Tyus 1987; Marsh and Minckley 1989; Bestgen et al. In review).

Declines in distribution and abundance of razorback sucker resulted in its listing in 1991 as federally endangered (U.S. Fish and Wildlife Service 1991). A recovery plan was drafted in 1998 (U.S. Fish and Wildlife Service 1998) and recovery goals were added in 2002 (U.S. Fish and Wildlife Service 2002). The goals state that each of the Upper and Lower Colorado River basins should maintain two "genetically and demographically viable, self-sustaining populations" for a five-year period before downlisting the razorback sucker to threatened status. In the UCRB, one would be located in the Green River subbasin and the other in either the upper Colorado River subbasin or the San Juan River subbasin, and abundance of adults in each subbasin is to exceed 5,800 individuals. Population stability and abundance levels must be sustained for another three years after downlisting as minimally sufficient conditions for delisting to occur.

At the time razorback sucker recovery goals were written, populations were deemed so imperiled that the first management action listed toward achieving recovery was to "Reestablish populations with hatchery-produced fish" (U.S. Fish and Wildlife Service 2002). Propagation and stocking began in 1995, but accelerated as consistent hatchery goals were established for the UCRB (Nesler et al. 2003). The stocking plan was amended as studies evaluating survival of hatchery-reared razorback suckers found low first-year survival and recommended stocking larger individuals in seasons other than summer (Zelasko et al. 2009; Zelasko et al. 2010; Zelasko et al. 2011; Integrated Stocking Plan Revision Committee 2015).

Razorback sucker larvae have been consistently captured by drift net and light trap sampling in the UCRB since 1992, but the first substantial captures after most wild fish were extirpated occurred in 2004, indicating stocked fish are spawning. However, wild-produced fish that reach sexual maturity and produce wild offspring have not been documented. Suspected biotic and abiotic mechanisms driving reduced recruitment and decline are hypothesized to occur in every life stage (Bestgen et al. 2007b). Low numbers of reproducing adults, impediments to spawning migrations, reduced flows and temperatures downstream of dams, and egg-predation by nonnative species all influence the timing and success of spawning (McAda and Wydoski 1980; Wick et al. 1982; Marsh 1985; Marsh and Minckley 1989; Modde et al. 1996). Reduced nursery habitat availability due to lower spring peak flows, variable and reduced temperatures of dam-released flows, and predation by nonnative species are thought to influence survival of early life stages (Tyus 1987; Minckley et al. 1991; Mueller et al. 2003; Bestgen 2008). These factors, singly or synergistically, are thought to inhibit most survival to the juvenile life stage (Holden et al. 2000). Recently, however, several thousand razorback sucker juveniles have been produced and returned to the Green River from wild larvae entrained into Stewart Lake, a floodplain wetland of the Green River, Utah, which was used to successfully demonstrate the principles of discharge timing and magnitude required for larval entrainment, as described in the Larval Trigger Study Plan (Bestgen et al. 2011; Skorupski et al. 2013; Schelly et al. 2014; Schelly and Breen 2015; Schelly et al. 2016).

In addition to limited production of juveniles, there have been increased numbers of adult razorback sucker captures in various sampling efforts (Bestgen et al. 2012a; Bestgen et al. 2013) and detections of fish at large for several years after stocking in the UCRB (Species Tagging, Research, and Monitoring System [STReaMS], https://streamsystem.org). Both may signify higher post-stocking survival of hatchery-reared individuals (which constitute most, if not all, of the existing UCRB population) after implementation of recommendations from Zelasko et al. (2009, 2011) in the species' revised stocking plan (Integrated Stocking Plan Revision Committee 2015). Furthermore, stocked individuals have been found to travel from the San Juan River, through Lake Powell, and upstream into the Green or Colorado rivers (Durst and Francis 2016), and spawn not only in historical Green and lower Yampa River mainstem locations, but also in the Colorado and San Juan River arms of Lake Powell (Durst and Francis 2016; Albrecht et al. In press) and the White River, a Green River tributary where adult presence was historically low and larvae had not been captured until 2011 (Webber et al. 2013).

In response to increases in razorback sucker captures throughout the UCRB, Bestgen et al. (2012b) used records of razorback sucker captures during Colorado pikeminnow abundance estimation sampling from 2006–2008 to assess the utility of using that data to estimate razorback sucker population parameters. That data produced imprecise survival rate and abundance estimates with wide confidence intervals and high coefficients of variation, largely due to few within-year recaptures and resultant low capture probabilities. The study concluded that "the type of data gathered in those three years, in and of itself, may be insufficient to adequately estimate demographic parameters of interest for razorback suckers in the Green River Basin." However, ever-increasing captures of razorback suckers during Colorado pikeminnow sampling in 2011–2013, along with larval survival due to floodplain wetland connections and an ongoing status assessment for the species, were sufficient impetus to pursue parameter estimation once again. Thus, this study used mark-recapture data collected during Colorado pikeminnow abundance estimate sampling, 2011–2013, to estimate survival rates, transition rates, capture probabilities, and abundance for razorback suckers in the Green River.

Goal and objectives

The goal of this study was to understand whether data collected during Colorado pikeminnow abundance estimation sampling was adequate to effectively describe demographic parameters for razorback suckers in the Green River basin. Objectives to accomplish that goal were to:

1. Compile and proof data for razorback suckers captured during Colorado pikeminnow abundance estimate sampling,
2. Identify covariates and effects for data analysis, and
3. Analyze data with appropriate parameter estimation software to obtain the most unbiased and precise survival rate and abundance estimates possible.

Results will aid managers attempting to recover razorback sucker and constitute a necessary first step in monitoring the Green River population amid increased catch rates and higher recruitment potential.

METHODS

Data

Razorback sucker data for this study was collected as a secondary objective during mark-recapture sampling for abundance estimation of Colorado pikeminnow in the Green River basin, UCRB Endangered Fish Recovery Program project #128 (Bestgen et al. 2007a; Bestgen et al. 2010). We obtained all data from the centralized UCRB database, created in Microsoft Access and maintained by U. S. Fish and Wildlife Service (USFWS), Grand Junction, Colorado. Data now resides in the Species Tagging, Research, and Monitoring System (STReaMS, https://streamsystem.org), an online database created for the management of data from the UCRB and San Juan River Basin recovery programs.

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 Lees 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 basin. Channel morphologies vary 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 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. 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 historic levels (Figure 2). Recent low flow years have 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, have been implemented since 2006 (U.S. Bureau of Reclamation 2006) and revisions have been experimentally applied to further enhance endangered fishes (Bestgen et al. 2011).

The study area was divided into three reaches: Green River from the mouth of Whirlpool Canyon downstream to near the White River confluence (“Middle Green River”, RK 539.4–396.0 [RM

334.0–246.0], excluding Split Mountain Canyon); Green River from the White River confluence downstream to near Green River, Utah, including Desolation and Gray canyons ("Desolation-Gray", RK 395.9–206.1 [RM 245.9–128.0]); and Green River from Green River, Utah, downstream to the Colorado River confluence ("Lower Green River", RK 193.2–0 [RM 120.0–0]; Figure 1). Colorado pikeminnow sampling also included reaches in two tributaries, Yampa and White rivers, but those were excluded from this parameter estimation due to scarcity of razorback sucker captures.

Sampling

Sampling was conducted from mid-April to late May from 2011 to 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", usually 7 to 11 days each) were attempted during each of the three study years. One pass could not be completed in the Middle Green River reach in 2011, because high water levels prevented boats from going under bridges. Electrofishing of near-shore habitat by hard-bottomed boat (Middle and Lower Green River reaches) or inflatable raft (Desolation-Gray reach) began at the top of each reach and proceeded downstream, using one craft per shoreline. Electrofishing units were either pulsed-DC Smith-Root or ETS Electrofishing Systems, LLC, units, with one or two booms with spherical anodes affixed to rafts or boats, respectively. Two watercraft were typically used on each sampling occasion, one on each shoreline, and one or two netters captured stunned fish. Approximately 7 to 10 d elapsed between passes in each reach to allow for sufficient mixing of marked and unmarked fish.

Similar to handling of Colorado pikeminnow, the primary species of interest in this sampling program (Bestgen et al. 2013), all captured razorback suckers were measured (TL, nearest mm), weighed (nearest g), scanned for the presence of a PIT tag, and tagged (when necessary) with a PIT tag just posterior to the pelvic girdle. Capture locations were determined (nearest 0.15 RK) from river maps and a Global Positioning System unit and release locations were within 0.15 km of capture, whenever possible.

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). The robust design allows estimation of multiple population parameters through the use of relatively longer (e.g., annual) primary sampling sessions and more closely spaced secondary sampling occasions (passes); the multi-state component estimates transition rates (movement) among reaches between the annual sampling sessions.

Parameters estimated in the primary ("open population") sampling sessions included: *S*, probability of survival from the start of one sampling session (year) 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, psi, probability of transition from one state (reach) to another. Parameters estimated in the secondary ("closed population") sampling occasions (passes) included *p*, probability of initial capture during the sampling session (year), and *c*, probability of recapture during the same sampling session. Although all razorback suckers in this study were essentially "recaptured" after first being tagged and stocked, "capture" and "recapture" will hereafter denote initial capture and subsequent capture (as described above) during this 2011–2013 period, unless otherwise stated. To include individual covariates, such as fish length (Bestgen et al. 2010) which affects capture probability, population abundance (*N*) was conditioned out of the likelihood using Huggins closed capture models and, instead, was a derived parameter.

Key assumptions under the closed robust design include: (i) there are no additions or deletions of animals across secondary sampling occasions and (ii) survival probability is the same for all individuals in the population, regardless of availability for capture. Key assumptions of multi-state models are: (i) survival is modeled with the survival probability for the state where the animal was captured, and then movement to a new state takes place and (ii) all individuals make transitions at the same time.

Covariates

Variables thought to affect razorback sucker survival and capture probabilities include fish size and condition, environmental factors, and time since stocking. The effect of fish length on capture probability and other parameters is generally an important feature of capture-recapture studies of fishes (Peterson et al. 2004; Dauwalter and Fisher 2007; Korman et al. 2009), including razorback sucker population dynamics studies (Marsh et al. 2005; Zelasko et al. 2010; Zelasko et al. 2011; Bestgen et al. 2012b; Kesner et al. 2017). Therefore, razorback sucker lengths at initial capture during the study as well as lengths at stocking were included as individual covariates. When records were missing capture lengths (0.5% of individuals), we used mean length of fish in the entire dataset, 404 mm total length (TL). When records were missing length at stocking (0.2% of individuals), we used mean batch length for razorback suckers stocked during the same event.

Year of stocking was included as an individual covariate as a surrogate for environmental and/or hatchery conditions at the time of stocking. Effects of those conditions on subsequent razorback sucker survival would be separate and different from those produced by environmental conditions or sampling variation during the study, portrayed simply by time variation within model structures (see *A priori model set*, below). Year of stocking also allowed us to calculate each razorback sucker's time at large between stocking and initial capture during the study.

A priori model set

We used the previously identified reaches and covariates to build an a priori model set. Additional effects were modeled directly within Program MARK. Survival rate, *S*, model structures included the following effects:

constant – no variation; constant survival rate estimate for all individuals and years across the study period;

year – survival rate estimates varied annually;

reach – survival rate estimates varied by river reach of capture;

TL at capture – survival rates estimates were (linearly) related to TL at initial capture during this study; squared (TL^2) and cubed (TL^3) terms were added to model the more plausible relationship of survival changing with increasing TL;

TL, TL^2, TL^3 at stocking – survival rates estimates were (linearly) related to TL at time of stocking;

year of stocking – survival rate estimates varied by year during which captured individuals were stocked;

at large – survival rate estimates varied by time since stocking (< 1 year, > 1 year); this effect stemmed from the "first year in the river" effect in our previous studies of stocked razorback sucker survival (Bestgen et al. 2009; Zelasko et al. 2010; Zelasko et al. 2011), which showed that more recently stocked fish had lower survival rates, presumably due to lack of predator avoidance, current conditioning, or other survival skills.

Transition probability, ψ, model structures included the following effects:

constant – no variation; constant probability of movement for all individuals, reaches, and years across the study period;

reach – probability of movement from one reach to another between years *t* and *t*+1 varied by river reach of capture at time *t*; because transitions are modeled as occurring only annually, within-year reach changes (n =5) were reassigned back to first capture reach for that year;

year – probability of movement from one reach to another between times *t* and *t*+1 varied by year of capture at time *t*.

Capture probability (initial), *p*, model structures included the following effects:

constant – no variation; constant capture probability estimate for all individuals, years, and passes across the study period;

reach – capture probability estimates varied by river reach of capture;

year – capture probability estimates varied annually;

pass - capture probability estimates varied by sampling pass;

TL at capture (TL, TL^2, TL^3) - capture probabilities were related to TL at first capture during this study;

TL at stocking (TL, TL^2, TL^3) - capture probabilities were related to TL at time of stocking.

Recapture probability, *c*, model structures were all set identical to initial capture probability, *p*, structures ($c = p$) due to paucity of recaptures necessary to model more complex scenarios.

Run procedure and model selection

For each parameter, effects were modeled individually, additively, and as interactions. We ran all models that contained the continuous individual covariate, TL, using the logit link to maintain a monotonic relationship. Alternatively, some models employed the sin link function, which was intended to aid estimation of real parameters with values close to zero or one. All transition probabilities were estimated using the multinomial logit link function, which constrains a set of parameters to sum to 1 or less. 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 and their overlap among pairs of estimates as an assessment of significance.

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 individuals were captured twice and 5 individuals were captured three times (Table 1). Reverse polarization of electrofishing rafts in the Lower Green River reach during 2013 and difficulties with sampling Middle Green River reach during high water in 2011 and low water in 2012 resulted in substantially lower catch rates in those years (Bestgen et al. 2017). Nevertheless, most individuals were initially captured in the Lower Green River reach (n = 1,742; 44% of individuals), followed by Desolation-Gray reach (n = 1,545; 39%) and Middle Green River reach (n = 655; 17%). A similar pattern emerged for the 208 individuals with multiple captures: nearly 60% (n = 123) of recaptures occurred in the Lower Green River reach, while only 33% (n = 69) and 8% (n = 16) occurred in Desolation-Gray and Middle Green River 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 River then Desolation-Gray (n = 10) or Desolation-Gray then Lower Green River (n = 9). The majority of all capture events (74%) occurred in 2011 and 2012, reflective of lower 2013 captures in Lower Green River reach (Table 2).

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 (Figure 3). Approximately 90% of lengths at capture were in the range between 325-475 mm TL. Similarly, 90% of lengths at stocking of those same captured fish fell in an even narrower range of 300-400 mm TL (mean: 349 mm, range: 177–470 mm).

Of all 3,932 individuals, 31% had been at large < 1 year between stocking and first capture in this study while 69% had been at large longer (18 months to nearly 13 years, Table 3). The ratios were similar for Desolation-Gray and Lower Green River reaches, with 33 and 37% of fish first captured in those reaches, respectively, at large < 1 year. In the Middle Green River reach, however, only 14% of razorback suckers captured were at large < 1 year since stocking. The year of stocking for captured fish ranged from 1998 to 2012 (Table 4). The majority (53%) of razorback suckers captured during the study had been stocked in 2009 or 2010, and 90% had been stocked in 2008 or later.

Model selection

The model with the lowest AIC_c value had 40 parameters (Table 5), carried 51% of AIC_c weight, and included effects of initial capture reach, study interval, study year, sampling pass, and time at large since stocking. The next closest model was within 3 AIC_c units of the top-ranked model but carried less than 12% of AIC_c weight. The only difference between the two models was the inclusion of the "time at large" effect in the top model. Due to the strong influence of a similar effect in our previous analyses and the low weight of the second-ranked model, the top-ranked model was chosen for further inference.

Parameter estimates

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 one "time at large" effect (Table 6). Due to very low numbers of recaptures between pairs of years in each reach (Table 7), precision of $\hat{S}$ was low, with some 95% CIs nearly spanning zero to one (Figure 4). However, the overarching effect of "time at large since stocking" was evident. The estimated coefficient for the effect was positive and its 95% confidence interval did not overlap zero (0.96, 0.03–1.89; Table 6), resulting in higher $\hat{S}$ for razorback suckers at large > 1 year in Middle Green River and Desolation-Gray reaches (Figure 4). Survival rate estimates were similar between Middle Green River and Desolation-Gray reaches from 2011–2012 within each at-large class and were 1.7 times higher for fish at large > 1 year. From 2012–2013, survival rate estimates were lower than 2011–2012 and were higher in Middle Green River reach than Desolation-Gray reach for both at-large classes. Estimates for suckers at large > 1 year during that interval were 2.4–3.8 times higher than those for fish at large < 1 year. The pattern for time at large was not maintained for Lower Green River reach survival rate estimates due to the behavior of the sin link function used to transform estimates, coupled with apparently high estimates for fish at large < 1 year in that reach (see DISCUSSION, *Time at large since stocking*).

Abundance— Estimates of abundance, $\hat{N}$, were generally highest in upstream Middle Green River reach (Figure 5). Annual estimates increased from 2011 to 2012 in all reaches, and declined from 2012 to 2013 in Middle Green River and Desolation-Gray reaches. Although the 2013 estimate in Lower Green reach is presented for completeness, we are doubtful of the presumptive increase from 2012 to 2013 given the sampling error and low catch rate of 2013. No estimate is significantly different from others, based on 95% confidence intervals. Annual estimates for the Green River basin (the three study reaches combined) ranged from 25,482–36,355 razorback suckers (Figure 6), but the same caution should be taken when viewing the 2013 estimate.

Transition probability—Razorback sucker transition probability estimates were modeled with six parameters, for each of the six possible transitions among the three reaches (Table 6). The probability of remaining in a reach was not estimated, but calculated by subtracting from 1 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, rather, illustrated possible trends in movement. Transitions out of Desolation-Gray reach were estimated to be the highest: 0.31 probability of moving to Middle Green River reach and 0.07 probability of moving to Lower Green River reach. The probability of transition from Lower Green River to Desolation-Gray reach was 0.10. All other ψ estimates were low, from near 0 (no actual transition was documented from Middle Green River to Lower Green River) to 0.03 (Table 8).

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 (Table 6). Mean $\hat{p}$ for the study was 0.02 (range: 0.002–0.056). Mean reach-wide $\hat{p}$ increased slightly from up- to downstream: 0.01 in Middle Green River, 0.02 in Desolation-Gray, and 0.03 in Lower Green River. Variation in $\hat{p}$ among reaches and years was considerable, but less so among passes within most reach/year combinations (Table 9). Highest $\hat{p}$ was in Lower Green River reach (0.06), while lowest was in Middle Green River reach (0.002), both during pass 1 of 2011 (Table 9).

Discussion

The few recaptures of razorback suckers during 2011–2013 sampling and resulting estimate imprecision lead us to conclude that data from Colorado pikeminnow abundance estimate sampling alone is not adequate to estimate population parameters for razorback suckers. Capture probabilities were very low and abundance, survival rates, and transition rates were estimated with little precision. Abundance estimates were highest but least precise in upstream Middle Green River reach and declined downstream. Time at large from stocking to capture was one of the influential factors, along with year and river reach, affecting survival rate estimates, with higher survival for those at large > 1 year in Middle Green River and Desolation-Gray reaches. Very few movements among reaches precluded meaningful transition rate estimates; however, most of those few movements (and highest transition rates) were out of Desolation-Gray reach and most movement was upstream. All parameter estimates for Lower Green River reach in 2013 were compromised by low probabilities of capture due to reverse polarization of electrofishing equipment. Below, we discuss possible reasons for, and implications of, these results.

Abundance

Abundance estimates from this analysis were imprecise, but increased since the 2006–2008 time period (Figure 6). The increasingly high numbers of razorback suckers stocked into the basin after 2006 (Table 4) likely explain the increase in abundance estimates. Furthermore, changes in stocking protocols (i.e., increasing mean total length of stocked fish to 300 mm; Shaughnessy 2010) also likely aided razorback sucker survival and abundance.

Total length

Total length of razorback suckers, either at time of stocking or first capture during this study, was not a significant effect on any parameter in this analysis. This was surprising, given the importance of TL in other analyses of razorback sucker survival (Marsh et al. 2005; Bestgen et al. 2009; Zelasko et al. 2010; Zelasko et al. 2011; Kesner et al. 2017). 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 the first intervals after stocking were positively associated with length at stocking. Thus, we first indirectly modeled length at stocking in this study using initial capture length as a surrogate, and also modeled the effect directly by retrieving stocking records of all razorback suckers in the dataset.

Capture length did not emerge as an influential effect on survival rates (or capture probabilities), so we further scrutinized the length data and found that 90% of fish lengths at capture fell in a relatively narrow range (325–475 mm TL). Survival rates generated for that TL range differed by 10% or less for each interval (Figure 7). Nearly 60% of capture lengths constituted an even narrower range (375–450 mm TL) and survival rate estimates for that range varied by only 4%. Adding capture length effects to capture probability model structures produced inestimable parameters, likely due to lack of data to support the more complex structure. Thus, lack of variation in capture lengths explained why that covariate was not useful in estimating models.

We also modeled length at stocking to compare its effect on survival to that in our previous studies (Bestgen et al. 2009; Zelasko et al. 2009; Zelasko et al. 2011) and to determine if length at stocking could explain differences in survival rates among reaches. The highest-ranked model including length at stocking in the survival structure fell more than 4 AIC_c points from the top-ranked model and carried only 6% of AIC_c weight (Table 5). Similar to capture lengths, we concluded that the low ranking of this effect was due to similarity among fish sizes: 90% of lengths at stocking fell between 300 and 400 mm TL and over 60% were between 325 and 375 mm TL. Survival rate estimate curves exhibited the expected relationship (increasing survival with increased length at stocking), but 95% CIs of all estimates spanned nearly the entire interval from 0 to 1. Our previous analysis of hatchery-reared razorback suckers included many years of stocking data (1995–2005) and, thus, more fish in smaller length categories (Figure 5 in Zelasko et al. 2009) than in the current analysis, which allowed for estimation of the length variable's effect on survival and capture probability. As stocking protocols have evolved in the UCRB to stock fewer but larger razorback suckers (Nesler et al. 2003; Integrated Stocking Plan Revision Committee 2015), this important variable may have become less useful in estimating population parameters. Furthermore, the few recaptures made during this study also hindered our ability to determine if/how fish size (at either stocking or capture) affected survival and capture probability. Nevertheless, differences in lengths at stocking and capture (Figure 3) demonstrate that surviving razorback suckers are able to adapt and grow after being stocked into the Green River, unlike bonytail *Gila elegans*, another Colorado River Basin endangered species stocked into the same river (Bestgen et al. 2008).

Notably, 213 individuals in our original dataset (4.8%) did not have stocking information associated with their tags and they were not recorded as recaptured fish in the field, meaning they were untagged at time of capture and implanted with new PIT tags. An additional 142 individuals with no associated stocking data were recorded as recaptures in the field, meaning they had tags upon capture that could not be traced back to a stocking event. Several possibilities could explain the lack of tags and/or stocking data: the razorback suckers were wild-produced fish, the "recaptured" designations were erroneous, the stocking data is not in the STReaMs database, the fish were not scanned for both types of PIT tags potentially present, tags were not detected by scanning equipment, or tags were not recorded correctly by field personnel or electronic data storage devices. Tag loss is another possible reason for some of the untagged fish records; tag loss in a controlled hatchery study was up to 5% (1 tag lost from each of 20 and 26 tagged fish batches) over an 18-month period (Burdick and Hamman 1993), which is similar to the percentage of fish captured with no tags in this study. Further investigation of individual records and, perhaps, original data files would be required to make any determination about the probability of those fish being wild-produced razorback suckers, provided that data even exists. If water chemistry differs sufficiently among hatchery sources and the Green River, chemical "fingerprinting" of definitively untagged fish may help identify their sources. Regardless, even if all untagged fish represented wild fish recruitment, the presumptive recruitment rates do not offset mortality rates of stocked fish (Zelasko et al. 2009; Zelasko et al. 2011).

We considered using fish condition at time of stocking as a factor affecting razorback sucker survival. However, only 11% of records contained fish weights and not all groups of fish were represented which prevented use of a condition covariate. Assessing changes in fish condition from stocking to later capture may provide a more useful metric in future survival analyses, especially because lengths of propagated individuals are becoming more consistent. The revised stocking plan for razorback suckers states, "Biologists will collect a length and weight sample of every batch of razorback sucker stocked to provide a length-weight relationship" (Integrated Stocking Plan Revision Committee 2015), but was not yet implemented at the time of this study. Inclusion of condition as a covariate in survival or other analyses is contingent on collecting that data at the time of stocking.

Time at large since stocking

The most influential effect on razorback sucker survival, other than year and reach of river, was time at large from stocking to first capture during this study. In both Middle Green River and Desolation-Gray reaches, razorback suckers at large > 1 year before capture survived at higher rates than those at large < 1 year. Overlapping 95% CIs among pairs of reaches, intervals, and at-large categories (Figure 4), however, preclude comparison of specific estimates and only allow discussion of trends. The pattern of lower survival for razorback suckers at large < 1 year before capture in both the Middle Green River and Desolation-Gray reaches supports similar findings from previous studies of the species' post-stocking survival. Marsh et al. (2005) estimated first-year survivorship to be ≤ 0.26 for most razorback suckers stocked in Lake Mohave from 1999–2002. Several 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 rate of 0.05, when averaged across stocking season, while 300-mm-TL fish were predicted to survive at a rate of 0.15 (Zelasko et al. 2009). Similarly-sized razorback suckers stocked during the 2004–2007 study period had a predicted mean survival rate of 0.09 (Zelasko et al. 2011). We found the same pattern in the San Juan River using data from 1994 through 2008 (Bestgen et al. 2009), where first-year survival varied annually but was always lower than subsequent-year survival.

The pattern of higher survival for razorback suckers at large > 1 year before capture was not maintained in the Lower Green River reach due to the behavior of the sin link function used to transform estimates, coupled with apparently high survival estimates for fish at large < 1 year in that reach. Use of the sin link was intended to aid estimation of parameters that were near boundaries of the 0–1 interval. Our addition of the "at large > 1 year" effect tipped the already high "at large < 1 year" estimates past one and then back down into the 0–1 interval, as expected, because of the cyclical nature of the sin function. However, the "> 1 year" estimates remained in the lower end of the interval, resulting in lower estimates for fish at large > 1 year (Figure 4) and signifying that the sin link did not perform much better than the logit link when transforming these poorly estimated parameters. The non-intuitive high survival rate estimates for razorback suckers at large < 1 year in Lower Green River reach may have resulted from relatively high initial capture rates of those fish during all years (Table 3) combined with substantially higher recaptures of most annual cohorts (Table 7).

The trend of low first-year survival for stocked razorback suckers in this study and others is 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, constant 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* Richardson) stocked into the Kootenai River, Idaho, exhibited first-year survival rates 30% lower than in subsequent years (Ireland et al. 2002; Justice et al. 2009). A brown trout 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 bonytail have such low return rates after being at large > 6 months that post-stocking survival is assumed to be extremely low (Badame and Hudson 2003; Bestgen et al. 2008). Genetic analyses of razorback sucker hatchery stocks throughout the Colorado River Basin may provide further insight into variable survival rates (Dowling et al. 1996; Dowling et al. 2012).

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 to be stocked, but increasing mean TL at stocking from >300 mm to >350 mm. The plan also called for an intensive rearing method (a combination of outdoor ponds during warmer month and indoor tanks or runs in the winter to increase growth) and stocking in seasons other than summer, recommendations from Zelasko et al. (2009, 2011). Finally, the plan suggests, but does not require, flow acclimation and predator recognition/avoidance training to further increase survival probability of recently stocked individuals. Hatcheries have reached target numbers and sizes nearly every year since 2013 (Bingham et al. 2013; Schnoor and Fry 2013; Bingham et al. 2014; Schnoor and Fry 2014; Bingham et al. 2015; Schnoor and Fry 2015; Bingham et al. 2016; Schnoor and Fry 2016), but conditioning suggestions have not yet been implemented. Any conditioning experiments undertaken should employ carefully crafted study designs (e.g., Kegerries and Albrecht 2009; Senger and Sjoberg 2011) to allow meaningful post-stocking survival evaluations in the future.

We note that higher survival rates after razorback suckers' first years post-stocking are adequate to maintain the Green River population at the level described in the species' recovery goals, but stocking would have to continue in perpetuity in the absence of natural recruitment. Managers should consider how to best use limited resources, but improving first-year survival of stocked razorback suckers may be a necessary expenditure until marked improvements in recruitment have been achieved.

Year and season of stocking

Although the year fish were stocked was not an important predictor of razorback sucker survival, we found that most fish captured between 2011 and 2013 had been stocked in either 2009 or 2010 (Table 4). The finding parallels data collected in 2012 and 2013 from antenna arrays located at a known spawning area in Middle Green River reach, in which most fish detected in 2012 had been stocked in 2008 or 2009 (69%; Webber and Jones 2012) and most detected in 2013 had been stocked in 2008, 2009, or 2010 (87%; Webber and Jones 2013). Data from the spawning bar, however, represents primarily spawning individuals so it is not surprising that fish at large for several years would be better represented than those stocked only a year or two prior (Bestgen and Jones 2017). In contrast, most razorback suckers physically captured anywhere in the UCRB between 1996 and 2006 had been stocked within the previous year or two (mean: 83%, range: 51–100%, annually; KAZ unpublished data). In this study, annual captures of fish that had been stocked within the previous two years were lower (mean: 52%, range: 23–74%) and individuals stocked three or four years prior to capture were better represented (Table 4). Again, greater uniformity and increases in length at stocking may have attenuated the trend of primarily capturing more-recently stocked fish (since length at stocking greatly affected survival in earlier studies), and there were no notable differences in size of razorback suckers stocked in 2009 and 2010 compared to 2011 or 2012 (STReaMS, https://streamsystem.org). Furthermore, there were not large differences in numbers of razorback suckers stocked per year since 2006 (mean: 19,711, range: 16,286–21,428; Table 4). However, the ratio of fish stocked into Middle

Green River compared to Lower Green River was highest in 2009 (3:1; Table 4). Environmental factors at the time of stocking, such as discharge, may also help explain differences in capture rates among stocking years, since mean daily flows of the Green River in 2009 and 2010 were intermediate between very high discharge years such as 2011 and very low years such as 2012.

Another factor that differed among recent years was season of stocking. We found in previous analyses that stocking razorback suckers during summer months (June through August) was detrimental to survival (Zelasko et al. 2009; Zelasko et al. 2011). From 2006 through 2012 (years with similar numbers of fish stocked), the lowest proportion of razorback suckers stocked during summer was in 2009 (< 1%), followed by 2010 (23%); proportions in other years ranged from 25–56% (Table 10). The lower summer proportions may have contributed to higher contact rates of razorback suckers stocked in those years. However, effects of season and discharge may be confounded, since nearly all 2009 fish were stocked during autumn and after higher snowmelt run-off flows had ended. The Revised Integrated Stocking Plan (2015) states that fish will not be stocked during summer months, so we expect the season of stocking effect to become less influential on razorback sucker survival estimates in the future.

Transition probability

Razorback suckers moved out of Desolation-Gray reach at higher rates than any other reach (total ψ = 0.38), and most of those movements were upstream to Middle Green River reach (9 of 23 among-year reach changes; Table 8). Movement by razorback suckers to Middle Green River reach may be explained by migrations to known spawning areas. However, the disparity in movement rates among reaches was unexpected, given that no razorback suckers were stocked in Desolation-Gray reach (Table 4), and fish captured in that reach from 2006–2008 were never recaptured during those years (Bestgen et al. 2012b), implying very low survival. Thus, fish captured in Desolation-Gray reach must originate in another reach, and then move out again and be captured in order to transition to another reach. In fact, there was considerable movement from Lower Green River reach upstream to Desolation-Gray during this study (10 of 23 among-year reach changes; ψ = 0.10), but very little from Middle Green down to Desolation-Gray (1 of 23; ψ = 0.03). The low number of observed reach changes limits inferences that can be made from this data.

The preponderance of upstream movements contradicted results from our previous analysis, 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, and most movement (longest distances and highest rates) occurred between stocking and first capture (Zelasko et al. 2009). It may be that after initial downstream travel, possibly due to lack of flow acclimation, razorback suckers are better able to maintain position and move upstream, if desired. Both Desolation-Gray and Lower Green reaches are downstream of stocking locations, and the proportions of razorback suckers captured each year that were stocked the previous year were higher in those two reaches than in Middle Green reach (Tables 3 and 4). Thus, fish stocked in summer or autumn may have moved (or been swept) downstream before initial capture during this study, and then were only found to move upstream upon subsequent capture. Regardless, we underscore that these movement patterns were based on few recaptures, and a finer-scale analysis of movement patterns including data from a broader area and longer time period would be more informative.

We investigated using data from the White River for this study, but too few captures precluded its inclusion. It is notable, however, that 11 among-year reach changes (the kind used for transition probability estimation) involved razorback suckers moving to or from the White River. Those would have added considerably to the 23 changes among the Green River reaches used in this study. Of the 11, seven changes were from Desolation-Gray reach to White River, further illustrating movement out of that reach. And, finally, there were seven within-year movements out of Desolation-Gray reach to White River, Middle Green River, and Lower Green River reaches (and a few out of others). Those within-year reach changes did not contribute to transition rate estimation, so the second capture event was assigned back to the original reach to aid in abundance estimation (which is calculated using within-year recaptures). Nevertheless, those reach changes provided even more evidence of higher rates of movement out of Desolation-Gray reach. It should be noted, too, that exclusion of information from the White River reduced overall numbers of recaptures, thereby affecting already low capture probabilities and contributing to biased/imprecise survival and abundance estimates (see *Capture probability*, below).

Capture probability

Recapture rate of razorback suckers during this study was extremely low: 208 (5.3%) of 3,932 individuals. Of those, 205 individuals were captured twice during the study: 107 were captured in different years and used for survival and transition rate estimation (Cormack 1964; Jolly 1965; Seber 1965; Brownie et al. 1993), while 98 were within the same year and used for abundance estimation (Pollock 1982; Kendall et al. 1995). The remaining three individuals were captured three times during the study, both within and among years, and contributed to both parts of the analysis. The among-year recapture rate (110 out of 3,932 individuals or 2.8%) was higher than in our previous analyses: 1.5% for razorback suckers stocked into the UCRB from 2004–2007 and 1.1% for those stocked from 1995–2005 (Zelasko et al. 2009; Zelasko et al. 2011). Within-year recaptures were not utilized in those survival analyses.

Low recapture rates accordingly resulted in low capture probability estimates (mean: 0.02, range: ~0.00–0.07). Capture probability is closely linked to survival estimation, because the probability of an individual razorback sucker's encounter history is the product of its survival rates and capture probabilities for all intervals and occasions. Similarly, capture probability strongly influences abundance estimates, due to the basic relationship:

$$\hat{N} = \frac{n}{p^*},$$

where $\hat{N}$ is the abundance estimate, n is the number of unique individuals encountered in a sample, and p^* is the probability of being captured one or more times. Not only might very low p estimates result in inflated estimates of N, but the low p estimates in this and our previous studies were also imprecise. Increasing capture probabilities and their precision results in more precise survival and abundance estimates (Seber 1986; Lebreton et al. 1992), so it is worthwhile to make improvements in those parameters if possible. In this study, we found that capture reach, year, and pass all affected capture probabilities.

Among reaches, capture probability estimates were highest in Lower Green River reach for 2011 and 2012, but dropped down to some of the lowest of the study in 2013 (Table 9) due to faulty equipment setup. Estimates were consistently low in Middle Green River reach. The capture probabilities corresponded to more captures in Lower Green reach and fewer in Middle Green reach, and followed a similar pattern for Colorado pikeminnow capture probability estimates generated from the same sampling effort: mean annual estimates were higher in Lower Green than Middle Green, except in 2013 when Lower Green sampling was affected by the same equipment problems and Middle Green had a particularly high estimate (Bestgen et al. 2017). This variation among reaches, though, is of little consequence when overall capture probabilities are miniscule.

The importance of sampling year on razorback sucker capture probability may have been driven largely by the equipment problem in Lower Green River reach, 2013. However, annual variation was also evident in Middle Green River reach. Capture probabilities in Middle Green River were particularly low in 2011 and 2012, perhaps reflecting the challenges to sampling completely and efficiently during exceptionally high (2011) and low (2012) flows (Figure 2; Bestgen et al. 2017), but a consistent pattern in capture probability estimates across reaches was not observed (Table 9). Fish behavior (learned gear avoidance) may also lead to annual variation in capture probabilities, 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 through time was the switch from Smith-Root to ETS electrofishing units, which began in 2011 and was completed in 2012 (and resulted in erroneous setup of the unfamiliar equipment in 2013). Electrofishing gear was swapped so field sampling could be conducted to minimize damage to fish caused by potentially harmful waveforms of electricity (Martinez and Kolz 2016). Differences in wave forms and electrofishing power among different gear and manufacturers may cause differences in catchability of fish. Biologists noted that Colorado pikeminnow were less stunned and more difficult to net using the new gear, which would reduce number of fish captured and recaptured. Regardless, capture probabilities for Colorado pikeminnow have declined since 2000 (Bestgen et al. 2017), long before sampling equipment was changed.

Similar to year, inclusion of the sampling pass effect on capture probabilities in the top model likely stemmed from a few larger differences (e.g., Desolation-Gray in 2012, Middle Green River in 2013). Variation among passes can similarly result from sampling efficiency (gear performance, crew experience, rising or dropping discharge levels) and fish behavior. Reasons for differences in already-minute capture probabilities among years and passes are difficult to ascertain but should be investigated further.

Fish length generally affects capture probability (Anderson 1995; Bestgen et al. 2007a; Dauwalter and Fisher 2007; Korman et al. 2009) and we demonstrated that for razorback suckers in past analyses. Capture probabilities increased for razorback suckers stocked at total lengths up to 390 mm and decreased for larger fish, which was concordant with actual recapture data (Zelasko 2008). That same relationship was revealed in this study, but the model incorporating TL into *p* structure was 3.5 AIC_c units away from the top-ranked model and carried less than 9% of model weight (Table 5). As with survival rate estimates, TL may have had little influence on capture probability estimates due to increased size uniformity of stocked razorback suckers in recent years.

Ultimately, increasing capture probability must become a priority if more precise parameter estimation is desired. While estimates are quite low, the relative size of the difference between some pairs of estimates is substantial and can dramatically affect other parameters. The influence of capture probability on abundance is clearly illustrated in Figure 5 where the lowest capture probability estimates resulted in inflated and highly imprecise abundance estimates, particularly in the Middle Green River reach. Changes in abundance estimates of the magnitude reported here should not be expected in these relatively large and longer-lived fish.

One reason for overall low capture probability estimates is that razorback sucker data for this study and our previous survival analyses had been collected as a secondary objective during Colorado pikeminnow abundance estimation sampling. Capture probability estimates were higher for Colorado pikeminnow than razorback suckers in each reach, year, and pass of the same sampling effort, even though the pikeminnow capture rates in the 2011–2013 period were among the lowest ever documented (Bestgen et al. 2017). In the same three reaches of the Green River as in this study, capture probabilities for Colorado pikeminnow ranged from 0.019 to 0.098 (annual means) and averaged 0.05 overall, higher than 0.02 for razorback suckers. Overall capture probability estimate for Colorado pikeminnow in the Colorado River subbasin in 2013 was also 0.05 (Osmundson and White 2017).

Future population parameter estimations would benefit from more consistent sampling efforts focused on razorback suckers, as defined by Bestgen et al. (2012b), particularly in years when intensive sampling for other purposes is not occurring. Additionally, data from PIT tag antenna arrays already in place throughout the UCRB would provide valuable encounter data, which may especially benefit survival estimates. For example, 530 unique razorback suckers were detected by a single array at the Green River canal in 2013 alone (STReaMS, https://streamsystem.org), which is nearly half of all 2013 capture events in this study. Furthermore, 93% of razorback suckers detected in 2012 and 2013 by antenna arrays at a known spawning area in Middle Green River reach had never been captured by other sampling efforts since being stocked (Webber and Beers 2014). In a study from the lower Colorado River, between Parker and Laguna dams, recapture rates of razorback suckers stocked from 2006–2008 were ≤9% using electrofishing and trammel netting, but increased to 39% when PIT tag antennas were employed (Schooley et al. 2008). A capture-recapture study on Lost River suckers in Oregon estimated low capture probabilities (0.02–0.15) when using only physical recaptures, but 0.91 or higher with high precision after employing a PIT tag antennas at known spawning locations (Hewitt et al. 2010). 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 under most simulated scenarios when data from PIT tag antennas were incorporated using the Barker model (Barker 1997) compared to Cormack-Jolly-Seber mark-recapture estimates. In another portion of the lower Colorado River, between Davis and Parker dams, inclusion of antennas increased captures to many times those from electrofishing and other routine monitoring methods and produced abundance estimates with relatively narrow 95% CIs (Kesner et al. 2017). It is important to note that increased recaptures via antenna detections may improve accuracy of survival estimates but only precision of abundance estimates (not the actual estimates of abundance). Furthermore, physical captures of razorback suckers would still be needed in order to analyze individual characteristics, such as TL or condition, and to document fish with no tags to monitor potential recruitment, so data from antennas should be employed alongside more traditional sampling methods.

Bias

Apparent survival differs from true survival in that apparent survival 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. Thus, $1 - S$ 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 basin, but razorback sucker encounters during other times of year (Bestgen et al. 2012a; Bestgen et al. 2013) and movement between the Green River and Lake Powell, Colorado River, and San Juan River (Durst and Francis 2016; Albrecht et al. In press), areas not included in this study, illustrate the pressing need to incorporate additional data. Increased capture and detection data would increase encounters of razorback suckers for analyses such as this and allow a more accurate representation of true survival. Increased encounters should, in turn, increase capture probability estimates and may allow estimation of recapture probabilities, potentially improving precision of survival and abundance estimates as suggested above.

CONCLUSIONS

- Abundance estimates of razorback suckers increased from 2006-2008 to 2011-2013, which was likely a product of continued or increased stocking through time and changes in stocking practices.
- Abundance estimates were highest, but least precise, in Middle Green River reach, and were lower in Desolation-Gray and Lower Green River reaches.
- Recaptures of razorback suckers during Colorado pikeminnow abundance estimation sampling were inadequate to produce precise abundance estimates.
- Survival of razorback suckers was generally higher for fish at large > 1 year from stocking to initial capture during this study, except in the Lower Green River reach where high capture and recapture rates of fish at large < 1 year since stocking hindered estimation of the effect.

- All abundance and survival estimates for the Lower Green River reach, 2013, are particularly unreliable due to equipment malfunction.
- Capture probabilities of razorback suckers were low for all reaches, years, and passes (0.02, on average), and lower than those of Colorado pikeminnow during the same sampling effort, which were also the lowest recorded since abundance estimation sampling began.
- Total length (capture or stocking) was not an important effect on razorback sucker survival or capture probability, likely due to the increased size uniformity of stocked fish.
- Transition probabilities were highest out of Desolation-Gray reach.

Recommendations

- Investigate ways to increase razorback sucker capture probabilities, such as: increasing sampling efforts for the species, sampling concentration areas more completely, and employing additional data from other subbasins, tributaries, projects, and gear (e.g., portable or fixed PIT tag scanning antennas already in place throughout the Upper Colorado River Basin).
- Investigate reasons for continued lower initial post-stocking survival of razorback suckers (e.g., fish condition, predator naïveté, and lack of flow acclimation).
- Collect razorback sucker length and weight data before fish are stocked if inclusion of condition indices is desired in future analyses.
- Continue to collect razorback sucker data from the White River and other tributaries and incorporate in future parameter estimation, when possible, to elucidate the role of tributaries in Upper Colorado River Basin population dynamics.
- Analyze razorback sucker encounter data (including other studies and PIT tag scanning antennas) at a finer scale and over longer periods and larger areas to more accurately depict the species' survival and movement patterns.
- Incorporate results of this study and future analyses into a razorback sucker monitoring program, which includes early life stages as well as adults.

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Table 1. Capture frequency of razorback suckers in the Green River, Utah, 2011–2013.

Capture frequency	Unique individuals	%	Capture events
1	3,724	94.7	3,724
2	203	5.2	406
3	5	0.1	15
Total	3,932	100.0	4,145

Table 2. Reach, year, and pass of all capture events (n = 4,145) of razorback suckers in three reaches of the Green River, Utah, 2011–2013. See Figure 1 for reach definitions.

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

Table 3. Percentages of razorback sucker individuals (n = 3,932) at large less than and greater than one year from stocking to initial capture during this study in three reaches of the Green River, Utah, 2011–2013. See Figure 1 for reach definitions.

Initial capture reach & year	At Large < 1 year	At Large > 1 year	Total
Middle Green River	14	86	100
2011	16	84	
2012	20	80	
2013	11	89	
Desolation-Gray	33	67	100
2011	41	59	
2012	27	73	
2013	33	67	
Lower Green River	37	63	100
2011	41	59	
2012	27	73	
2013	44	56	
All reaches	31	69	100

Table 4. 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.

	Middle Green River					Desolation-Gray					Lower Green River					total		
Year	stocked		captured, %			stocked		captured, %			stocked		captured, %			stocked		captured
of stocking	*n*	%	2011	2012	2013	*n*	%	2011	2012	2013	*n*	%	2011	2012	2013	*n*	%	%
1995	905	0.9														905	0.5	
1996	1067	1.1														1067	0.6	
1997		0.0																
1998	389	0.4	0.5													389	0.2	0.0
1999	1357	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		0.0																0
2002		0.0											0.1			274 *	0.2	0.0
2003	8492	8.6	7.1	4.5	2.2				0.4	0.5	2376	3.0	0.6	0.5	0.8	10868	6.1	1.1
2004	9621	9.7	5.7	3.8	2.6			1.7	0.6		5955	7.6	2.5	3.8	2.3	15576	8.8	2.2
2005	4864	4.9	6.7	1.5	1.3			1.0	0.6	0.5	4231	5.4	1.8	2.2	0.8	9095	5.1	1.6
2006	10079	10.2	1.4	2.3	1.0			0.7	0.1		10133	12.9	2.7	3.3		20212	11.4	1.4
2007	7748	7.8	5.2	4.5	3.5			7.3	2.8	0.9	8538	10.9	3.5	2.8	2.3	16286	9.2	3.4
2008	8387	8.5	17.6	11.4	12.1			15.3	14.6	7.1	10161	12.9	21.5	19.7	8.9	18548	10.4	15.6
2009	14269	14.4	37.1	37.9	28.1			32.6	19.7	14.9	5013	6.4	26.6	21.4	13.5	19282	10.8	24.1
2010	11404	11.5	15.7	12.9	25.9			41.4	34.2	26.8	10024	12.7	40.7	18.9	6.6	21428	12.1	29.1
2011	9089	9.2		20.5	12.1				27.1	16.7	12028	15.3		27.4	21.2	21117	11.9	13.8
2012	10912	11.0			10.9					32.7	10194	13.0			43.6	21106	11.9	7.4
total	98807	100	100	100	100			100	100	100	78653	100	100	100	100	177734 **	100	100

* stocking data for these fish contained no location information

** reach totals sum to 177460 due to 274 fish stocked during 2002 with no location information

Table 5. Robust design multi-state models to estimate survival rate (*S*), capture probability (*p*), transition rate (psi), 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. Effects in top models included: initial capture reach (reach), year, pass, time at large from stocking to initial study capture (AtLarge), initial capture length (TL, TL^2, TL^3), and length at stocking (stkTL, $stkTL^2$). See Figure 1 for reach definitions.

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

Table 6. Parameter estimates for the functions of sin *S* (survival rate), Mlogit ψ (transition rate), and logit *p* (capture probability) for razorback suckers captured in three reaches of the Green River, Utah, 2011–2013. MGR = Middle Green River, DGR = Desolation-Gray, LGR = Lower Green River. AtLarge = the effect on a fish of > 1 year elapsed from stocking to initial study capture. See Figure 1 for reach definitions.

Parameter	Description	Beta estimate	Standard error	95% confidence interval		
S	MGR, 2011-2012	0.136	1.712	-3.220	–	3.492
S	MGR, 2012-2013	-0.359	0.982	-2.283	–	1.565
S	DGR, 2011-2012	0.080	0.448	-0.797	–	0.957
S	DGR, 2012-2013	-0.745	0.329	-1.389	–	-0.101
S	LGR, 2011-2012	1.193	0.830	-0.433	–	2.820
S	LGR, 2012-2013	8.644	0.764	7.147	–	10.142
S	AtLarge	0.963	0.474	0.033	–	1.892
ψ	MGR to DGR	-3.353	1.121	-5.549	–	-1.157
ψ	MGR to LGR	-14.660	0.0	-14.660	–	-14.660
ψ	DGR to MGR	-0.671	0.562	-1.772	–	0.430
ψ	DGR to LGR	-2.161	0.779	-3.687	–	-0.635
ψ	LGR to MGR	-5.803	8.256	-21.984	–	10.379
ψ	LGR to DGR	-2.162	0.452	-3.049	–	-1.275
p	MGR 2011, pass 1	-6.146	1.013	-8.131	–	-4.161
p	MGR 2011, pass 2	-4.762	1.006	-6.734	–	-2.791
p	MGR 2011, pass 3	-5.198	1.005	-7.168	–	-3.228
p	MGR 2012, pass 1	-5.344	0.713	-6.741	–	-3.948
p	MGR 2012, pass 2	-6.115	0.723	-7.531	–	-4.699
p	MGR 2012, pass 3	-6.054	0.721	-7.468	–	-4.641
p	MGR 2013, pass 1	-5.670	0.509	-6.667	–	-4.673
p	MGR 2013, pass 2	-4.282	0.489	-5.239	–	-3.324
p	MGR 2013, pass 3	-3.833	0.489	-4.791	–	-2.874
p	DGR 2011, pass 1	-3.977	0.343	-4.648	–	-3.305
p	DGR 2011, pass 2	-3.759	0.342	-4.429	–	-3.089
p	DGR 2011, pass 3	-3.691	0.342	-4.361	–	-3.022
p	DGR 2012, pass 1	-4.342	0.240	-4.812	–	-3.871
p	DGR 2012, pass 2	-3.240	0.236	-3.704	–	-2.777
p	DGR 2012, pass 3	-4.398	0.241	-4.870	–	-3.926
p	DGR 2013, pass 1	-4.153	0.333	-4.805	–	-3.501
p	DGR 2013, pass 2	-3.671	0.331	-4.320	–	-3.022
p	DGR 2013, pass 3	-3.994	0.332	-4.645	–	-3.344
p	LGR 2011, pass 1	-2.829	0.152	-3.126	–	-2.532
p	LGR 2011, pass 2	-2.903	0.152	-3.201	–	-2.605
p	LGR 2011, pass 3	-2.875	0.152	-3.173	–	-2.578
p	LGR 2012, pass 1	-3.787	0.162	-4.104	–	-3.470
p	LGR 2012, pass 2	-3.791	0.162	-4.109	–	-3.474
p	LGR 2012, pass 3	-4.107	0.166	-4.432	–	-3.782
p	LGR 2013, pass 1	-5.904	0.590	-7.060	–	-4.748
p	LGR 2013, pass 2	-5.391	0.583	-6.535	–	-4.248
p	LGR 2013, pass 3	-4.694	0.580	-5.831	–	-3.556

Table 7. Recaptures of razorback suckers initially captured during this study 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 River 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.

Year	Released	Recapture Year		
		2011	2012	2013
		Middle Green River		
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 River		
2011	884	45	44	10
2012	643		17	6
2013	275			1

Table 8. Transition rate (ψ) estimates for razorback suckers captured in three reaches of the Green river, Utah, 2011–2013. See Figure 1 for reach definitions.

Transition			ψ	Standard error	95% confidence interval
Middle Green River	to	Desolation-Gray	0.034	0.037	0.004 – 0.239
		Lower Green River	0.000	0	0.000 – 0.000
Desolation-Gray	to	Middle Green River	0.314	0.119	0.134 – 0.576
		Lower Green River	0.071	0.051	0.017 – 0.256
Lower Green River	to	Middle Green River	0.003	0.022	0.000 – 1.000
		Desolation-Gray	0.103	0.042	0.045 – 0.220

Table 9. Capture probability estimates and 95% confidence intervals (in parentheses) for razorback suckers captured in three reaches of the Green River, Utah, 2011–2013. MGR = Middle Green River, DGR = Desolation-Gray, LGR = Lower Green River. See Figure 1 for reach definitions.

Reach	pass 1	pass 2	pass 3	Annual mean
		2011		
MGR	0.002 (0.000 - 0.015)	0.008 (0.001 - 0.058)	0.005 (0.001 - 0.038)	0.005
DGR	0.018 (0.009 - 0.035)	0.023 (0.012 - 0.044)	0.024 (0.013 - 0.046)	0.022
LGR	0.056 (0.042 - 0.074)	0.052 (0.039 - 0.069)	0.053 (0.040 - 0.071)	0.054
mean	0.025	0.028	0.028	0.027
		2012		
MGR	0.005 (0.001 - 0.019)	0.002 (0.001 - 0.009)	0.002 (0.001 - 0.010)	0.003
DGR	0.013 (0.008 - 0.020)	0.038 (0.024 - 0.059)	0.012 (0.008 - 0.019)	0.021
LGR	0.022 (0.016 - 0.030)	0.022 (0.016 - 0.030)	0.016 (0.012 - 0.022)	0.020
mean	0.013	0.021	0.010	0.015
		2013		
MGR	0.003 (0.001 - 0.009)	0.014 (0.005 - 0.035)	0.021 (0.008 - 0.053)	0.013
DGR	0.015 (0.008 - 0.029)	0.025 (0.013 - 0.046)	0.018 (0.010 - 0.034)	0.019
LGR	0.003 (0.001 - 0.009)	0.005 (0.001 - 0.014)	0.009 (0.003 - 0.028)	0.005
mean	0.007	0.014	0.016	0.013

Table 10. Percentages of razorback suckers stocked each season in the Green River basin, Utah, 1995–2012.

Year	Spring (Mar-May)	Summer (Jun-Aug)	Autumn (Sep-Nov)	Winter (Dec-Feb)
1995	0	0	100	0
1996	0	0	100	0
1997	0	0	0	0
1998	0	0	100	0
1999	0	54	46	0
2000	0	100	0	0
2001	0	0	0	0
2002	0	100	0	0
2003	71	0	29	0
2004	5	14	69	12
2005	3	31	66	0
2006	44	56	0	0
2007	2	35	63	0
2008	0	32	68	0
2009	< 1	< 1	99	0
2010	0	23	77	0
2011	< 1	33	67	0
2012	0	25	75	0

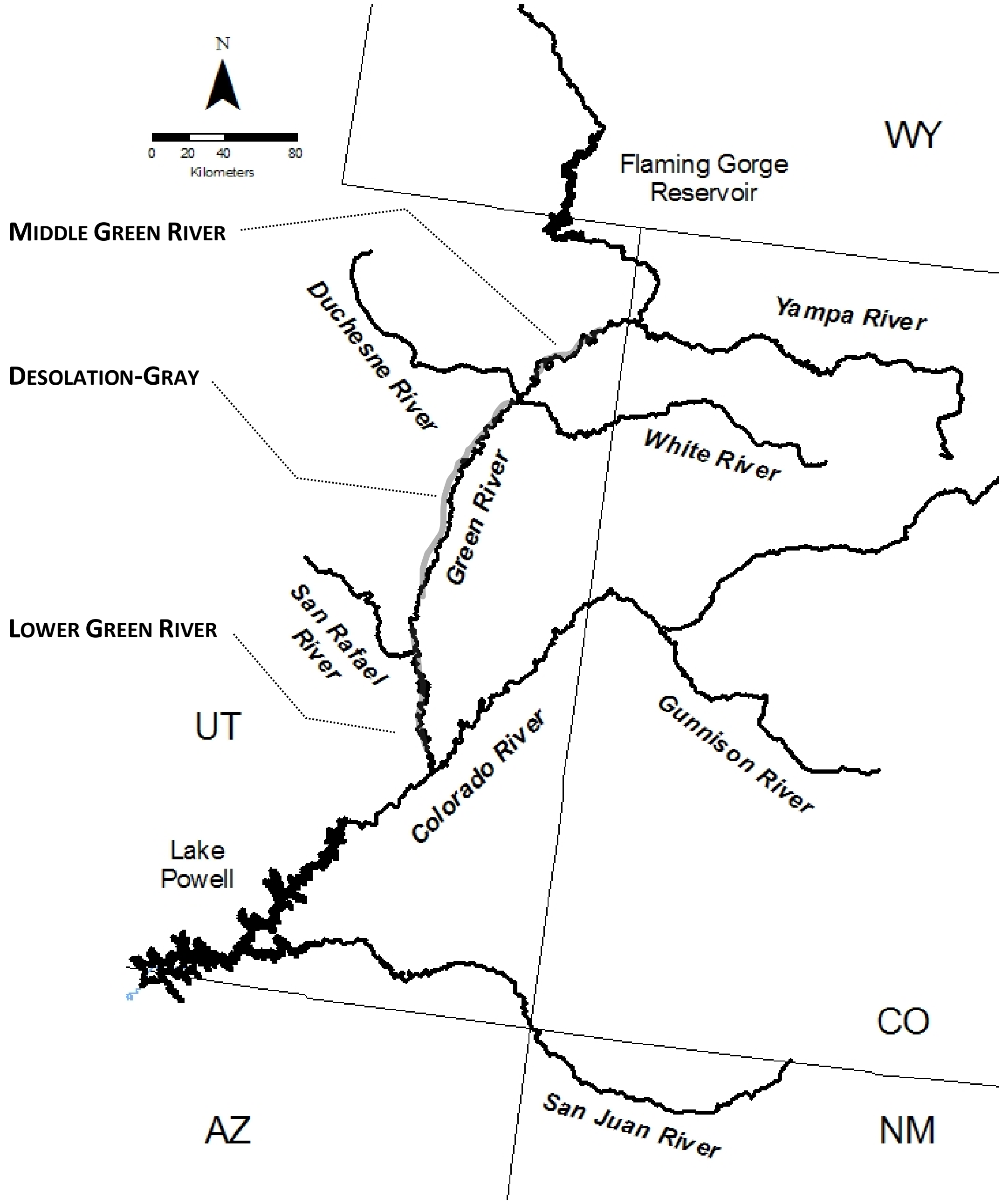

Figure 1. Map of the Upper Colorado River Basin, including three study reaches of the Green River, Utah. Middle Green River = Green River from the mouth of Whirlpool Canyon downstream to near the White River confluence (RK 539.4–396.0 [RM 334.0–246.0], excluding Split Mountain Canyon), Desolation-Gray = Green River from the White River confluence downstream to near Green River, Utah, including Desolation and Gray canyons (RK 395.9–206.1 [RM 245.9–128.0]), and Lower Green River = Green River from Green River, Utah, downstream to the Colorado River confluence (RK 193.2–0 [RM 120.0–0]).

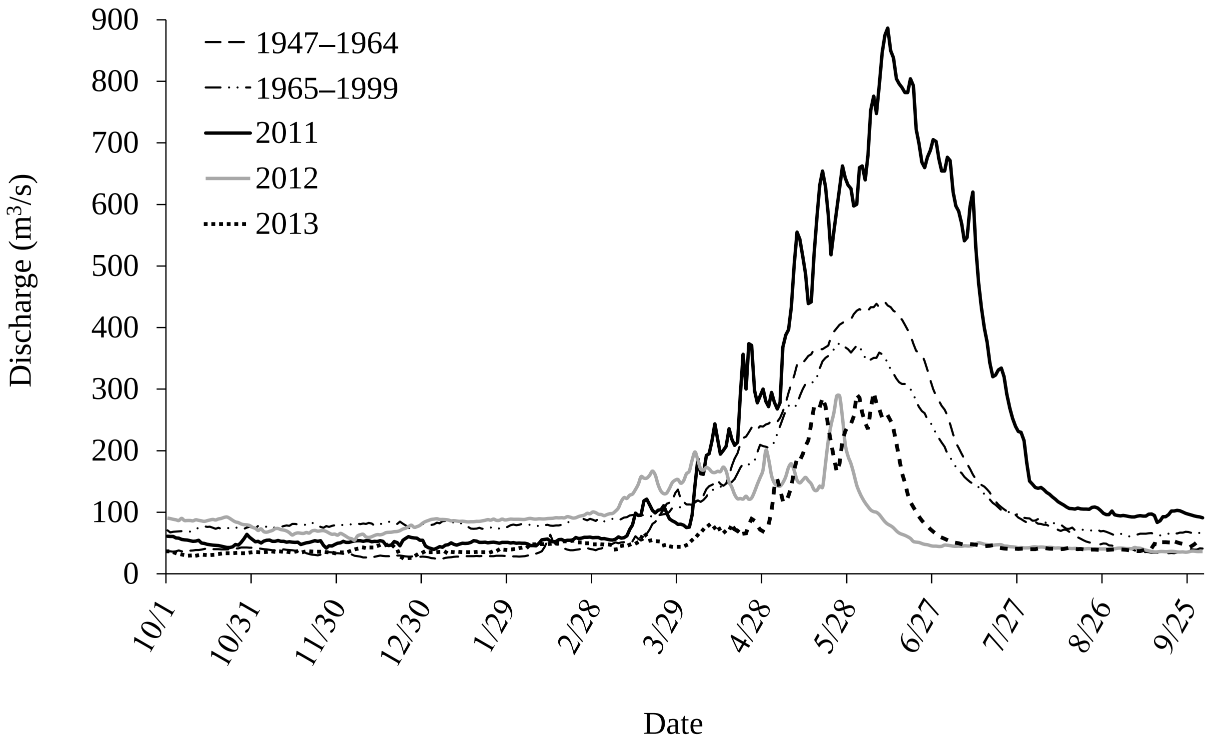

Figure 2. Mean daily discharge of the Green River near Jensen, Utah (U.S. Geological Survey gage 09261000), for water years 1947–1964 (pre-impoundment of Flaming Gorge dam), 1965–1999 (post-impoundment), and study years 2011–2013.

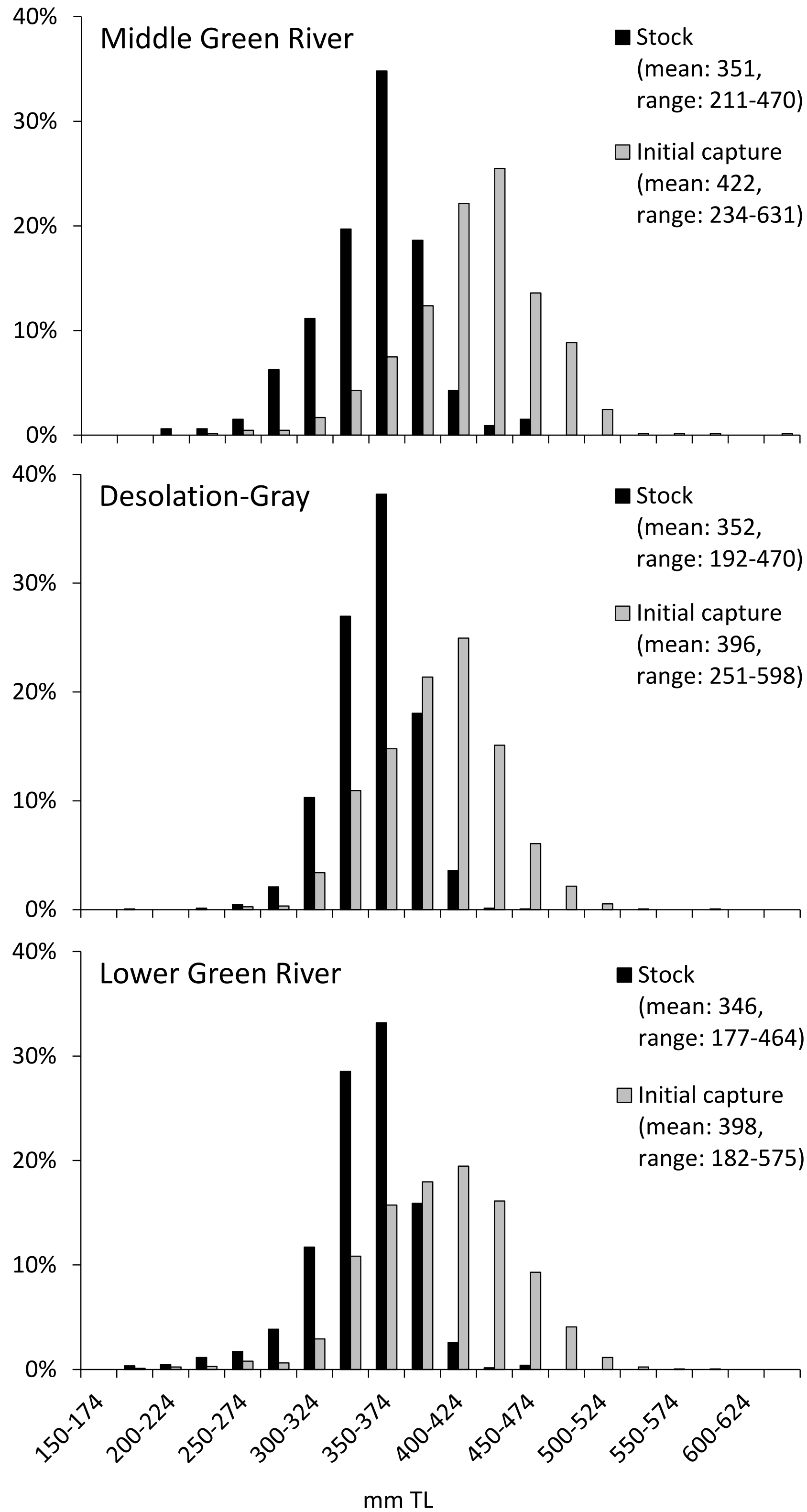

Figure 3. Total lengths at stocking and initial capture during this study for razorback suckers in three reaches of the Green River, Utah, 2011–2013. See Figure 1 for reach definitions.

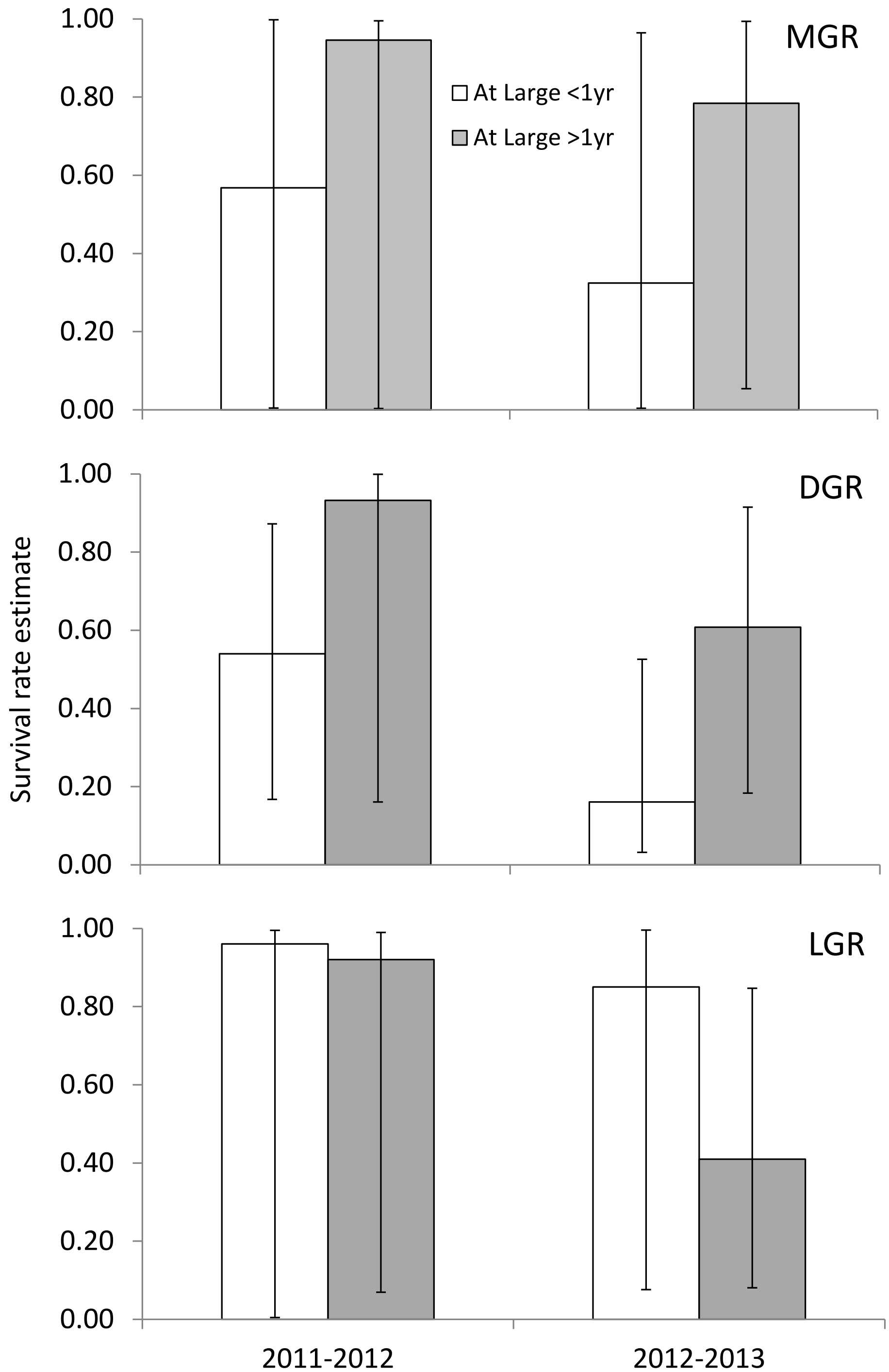

Figure 4. Survival rate estimates and 95% confidence intervals (vertical bars) by time interval and time at large from stocking to initial capture during this study for razorback suckers in three reaches of the Green River, Utah, 2011–2013. See Figure 1 for reach definitions.

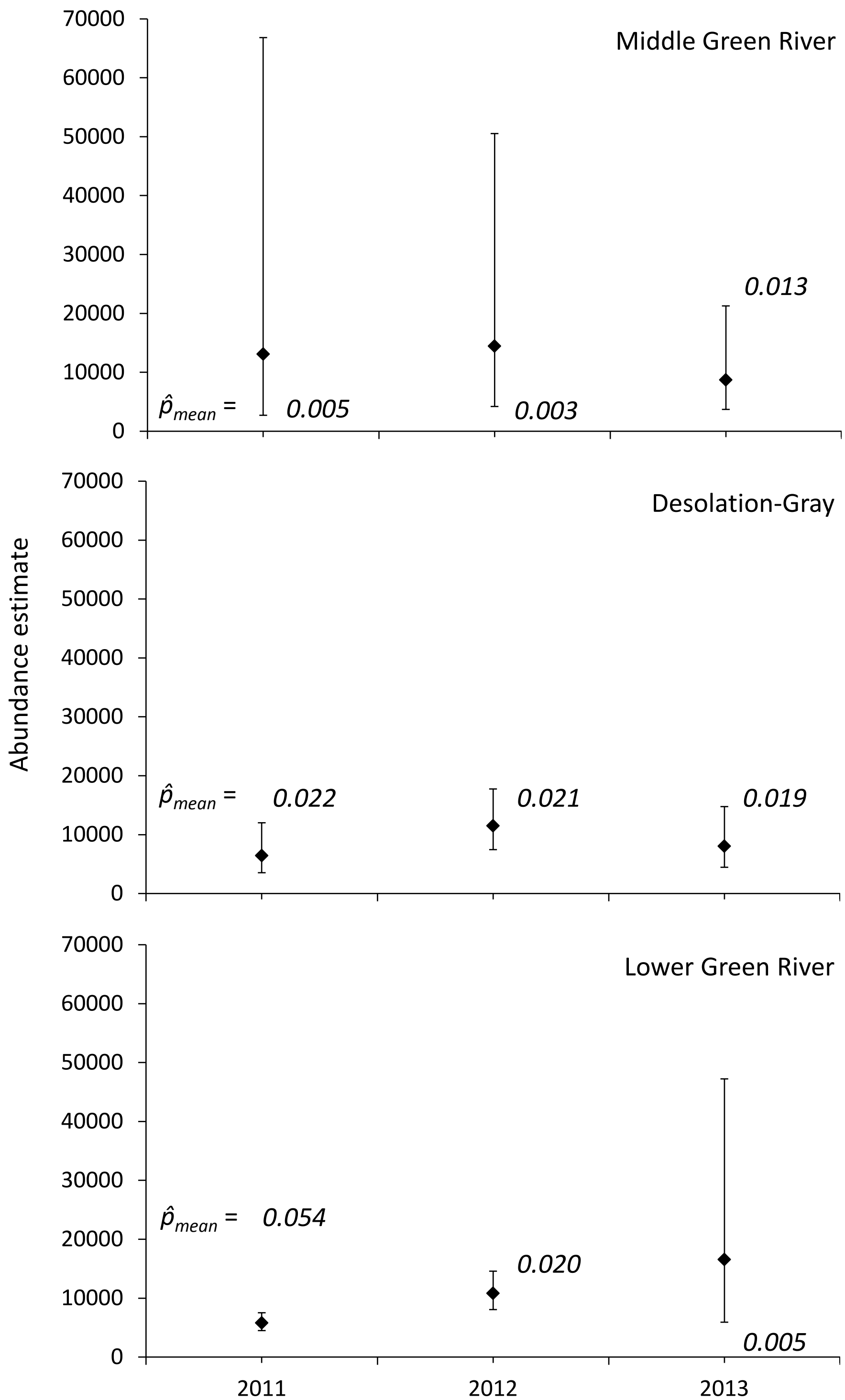

Figure 5. Abundance estimates, 95% confidence intervals (vertical bars), and associated mean annual capture probability estimates ($\hat{p}_{mean}$, average of sampling passes) for razorback suckers captured in three reaches of the Green River, Utah, 2011–2013. See Figure 1 for reach definitions.

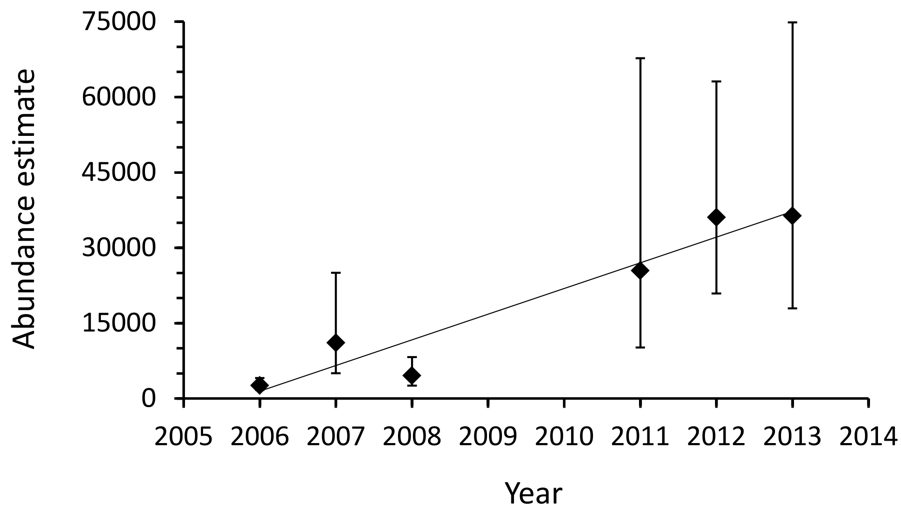

Figure 6. Model-averaged abundance estimates and 95% confidence intervals (vertical bars) for razorback suckers captured in the Green River, Utah, 2006–2013. Estimates are for Middle Green River, Desolation-Gray, and Lower Green River reaches combined and may differ slightly from sums of reach-specific estimates calculated without model averaging in this report and Bestgen et al. (2012). See Figure 1 for reach definitions.

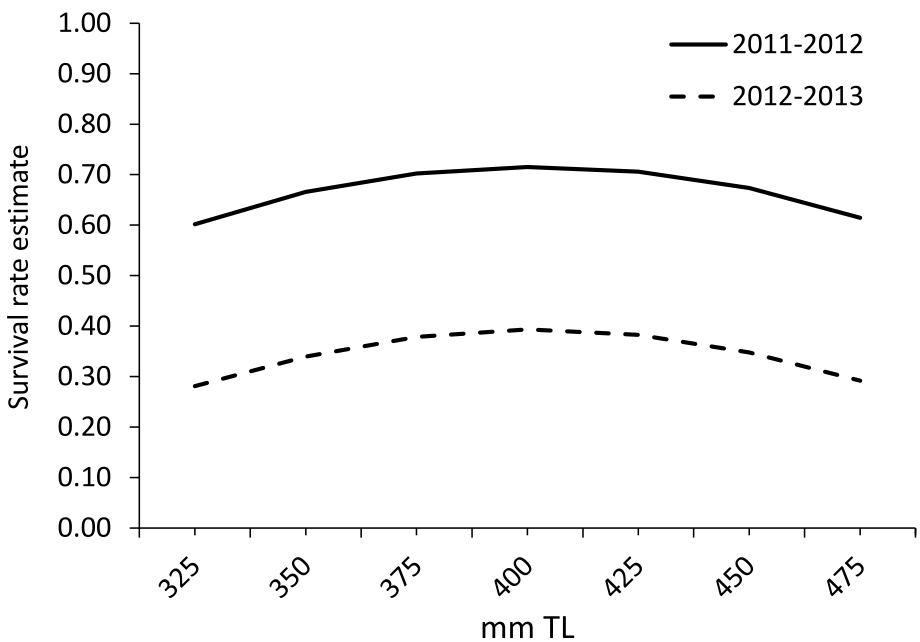

Figure 7. Length-dependent survival rate estimates for razorback suckers measuring between 325 and 475 mm TL at initial capture during this study (representing 90% of fish captured) in the Green River, Utah, 2011–2013.