Transactions of the American Fisheries Society 139:1478–1499, 2010

DOI: 10.1577/T09-107.1

[Article]

Survival Rates and Movement of Hatchery-Reared Razorback Suckers in the Upper Colorado River Basin, Utah and Colorado

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Abstract.—We used tag–recapture data to estimate apparent survival and capture probability for 119,129 hatchery-reared, federally endangered razorback suckers *Xyrauchen texanus* stocked into upper Colorado River basin streams during 1995–2005. Effects investigated included reach, year, and season of stocking; fish total length (TL) at time of stocking; survival in the first year after stocking versus in subsequent years; and sampling effort. Recapture data were also used to describe poststocking movement. First-year survival rate for stocked razorback suckers of average TL (252.5 mm) was low: 0.05 (95% confidence interval [CI], 0.042–0.071). Total length at stocking and first-year survival were positively correlated; survival approached zero for fish smaller than 200 mm TL but increased to 0.75 or higher for the few fish larger than 500 mm. Season of stocking had a large effect on razorback sucker first-year survival; the predicted rate for average-length fish stocked in summer was less than 0.02 (CI, 0.012–0.022), but it was 0.07 (0.044–0.094), 0.08 (0.057–0.100), and 0.08 (0.057–0.118) for fish stocked in spring, autumn, and winter, respectively. The overall subsequent-year survival rate for razorback suckers was estimated to be 0.75 (CI, 0.688–0.801). Capture probabilities were relatively low, ranging from 0.002 to 0.128 for fish of average TL. The mean minimum distance traveled, elapsed time, and rate of travel by razorback suckers between recaptures were 54.7 km (range, 0–514.9 km), 254 d (0–3,164 d), and 0.87 km/d (0–55.37 km/d), respectively. Movement was more frequent out of Colorado and Gunnison River stocking reaches (36.9%; range, 30.1–100%) than Green River stocking reaches (7.7%; range, 2.9–10.3%). Our recommendations include ceasing summer stocking, performing cost - benefit analyses of increasing TL at stocking, employing a standardized stocking protocol, and developing a comprehensive razorback sucker monitoring program, implementation of which should enhance recovery prospects for razorback suckers in the upper Colorado River basin.

The status and trajectory of an animal population depends on its demographic rates, such as births, deaths, and movement, as well as population size. Researchers investigating population change are often interested in estimating demographic parameters and understanding the factors that drive them. Endangered species management, in particular, relies on quantifiable population descriptors to guide conservation efforts and the recovery process. The highly modified Colorado River basin (Iorns et al. 1965; Van Steeter and Pitlick 1998) of the southwestern United States supports several endemic endangered species that are currently the focus of recovery efforts. One of these species, the razorback sucker *Xyrauchen texanus*, was once widespread and abundant from Mexico to Wyoming but 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).

Decline of razorback suckers coincided with multiple anthropogenic alterations to habitat and biota within the basin, such as dam construction and nonnative species introductions. Wild fish are rare and may be extirpated from the upper Colorado River basin (UCRB) above Glen Canyon Dam (Bestgen 1990; Bestgen et al. 2002). In the lower Colorado River basin, individuals are found primarily in Lake Mohave and Lake Mead, Arizona and Nevada (Marsh et al. 2003; Albrecht et al. 2008). However, the once large population in Lake Mohave was last estimated to number fewer than 3,000 fish (Marsh et al. 2003). Although larvae have been captured in the UCRB by drift net and light trap sampling, few juvenile razorback suckers have been encountered anywhere in the Colorado River basin (McAda and Wydoski 1980; Gutermuth et al. 1994; Bestgen et al. 2002; Marsh et al. 2005). Thus, recruitment failure is thought to be the primary reason for decline of the species throughout its

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Received June 18, 2009; accepted April 30, 2010
Published online September 22, 2010

range (Minckley 1983; Tyus 1987; Marsh and Minckley 1989).

Decline in distribution and abundance of razorback suckers resulted in the species' listing as federally endangered (USFWS 1991). A recovery plan was drafted in 1998 (USFWS 1998) and recovery goals added in 2002 (USFWS 2002) include maintenance of two "genetically and demographically viable, self-sustaining populations" in each of the upper and lower Colorado River basins. Abundance of adult razorback suckers in each population is to exceed 5,800 individuals for a 5-year period before they can be downlisted to threatened status. Population stability and abundance levels must be sustained for another 3 years after downlisting, which are the minimum conditions for delisting. Management strategies in both basins address habitat, instream flow, and nonnative species. However, without recruitment, protection of remnant adult populations and associated habitat would not be sufficient to prevent extirpation of razorback suckers. Therefore, the required self-sustaining populations can only be achieved with the aid of hatchery augmentation (USFWS 2002).

In response to the recovery goals and the need to evaluate success of razorback suckers stocked into the Green and Colorado river subbasins of the UCRB, stocking plans for the states of Utah and Colorado were integrated (Nesler et al. 2003). The San Juan River subbasin developed its own stocking plan, and it is not addressed here. The integrated UCRB plan recommends stocking razorback suckers at 300 mm total length (TL) or longer, advocates maintaining a minimum of four adult (age 4 or older, USFWS 2002) age-classes, and assumes survival rates of 0.50 for age-2 fish, 0.60 for age-3 fish, and 0.70 for adult fish. The assumed adult survival rate for stocked fish is consistent with that for wild individuals in the Green River, which was estimated at 0.71–0.76 (Modde et al. 1996; Bestgen et al. 2002).

A fundamental requirement of any recovery action, including stocking, is evaluation. Reviews of the UCRB endangered fish stocking plans began in the late 1990s. Studies relied on radiotelemetry (Burdick and Bonar 1997) and calculations of return rates (Burdick 2003; Francis and McAda 2006), but an insufficient number of recaptures of hatchery-reared razorback suckers prohibited evaluation of recovery goal survival rate assumptions. To date, many razorback suckers have been stocked and recaptured in the UCRB and data are sufficient for a robust analysis of stocked razorback sucker survival rates, which was the goal of this study. Specific objectives included: compilation of razorback sucker stocking and capture data, identification of strata and covariates for data analysis, analysis of data with appropriate parameter estimation software to obtain the most unbiased and precise survival rate estimates possible, comparison of survival rate estimates to those assumed in the integrated stocking plan, and analysis of razorback sucker movement to identify patterns that may affect stocking protocol.

Study Area

The upper Colorado River basin includes portions of Wyoming, Utah, Colorado, and New Mexico (Figure 1), and comprises the Green River, upper Colorado River, and San Juan River subbasins. The scope of this study is restricted to the Green and Colorado River subbasins. Channel morphologies vary from restricted, high gradient, canyon reaches to wide, braided, alluvial valley reaches. The region has a semiarid, 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 than historic levels. Storage reservoirs in the upper Colorado River create similar flow patterns in the downstream reaches. Recent low-flow years have resulted in spring peaks with reduced duration and magnitude (Figure 2), a factor that may affect reproduction and recruitment of several UCRB endangered fishes, including razorback suckers. However, flow recommendations intended to benefit endangered fishes in the UCRB, which would restore more natural base and spring peak flows to several rivers in the system, have either been implemented or are being formulated (Muth et al. 2000).

Methods

Data were analyzed in Program MARK (White and Burnham 1999) with the Cormack–Jolly–Seber open-population model (Cormack 1964; Jolly 1965; Seber 1965) and other closely related models. Model assumptions include: tagged individuals are representative of the population to which inference is made, numbers of releases are known, tagging does not affect survival, no tags are lost and all tags are correctly read, releases and recaptures are made within brief time periods relative to intervals between tagging, recapture does not affect subsequent survival or recapture, fates of individuals within and among cohorts are independent, individuals in a cohort have the same survival and

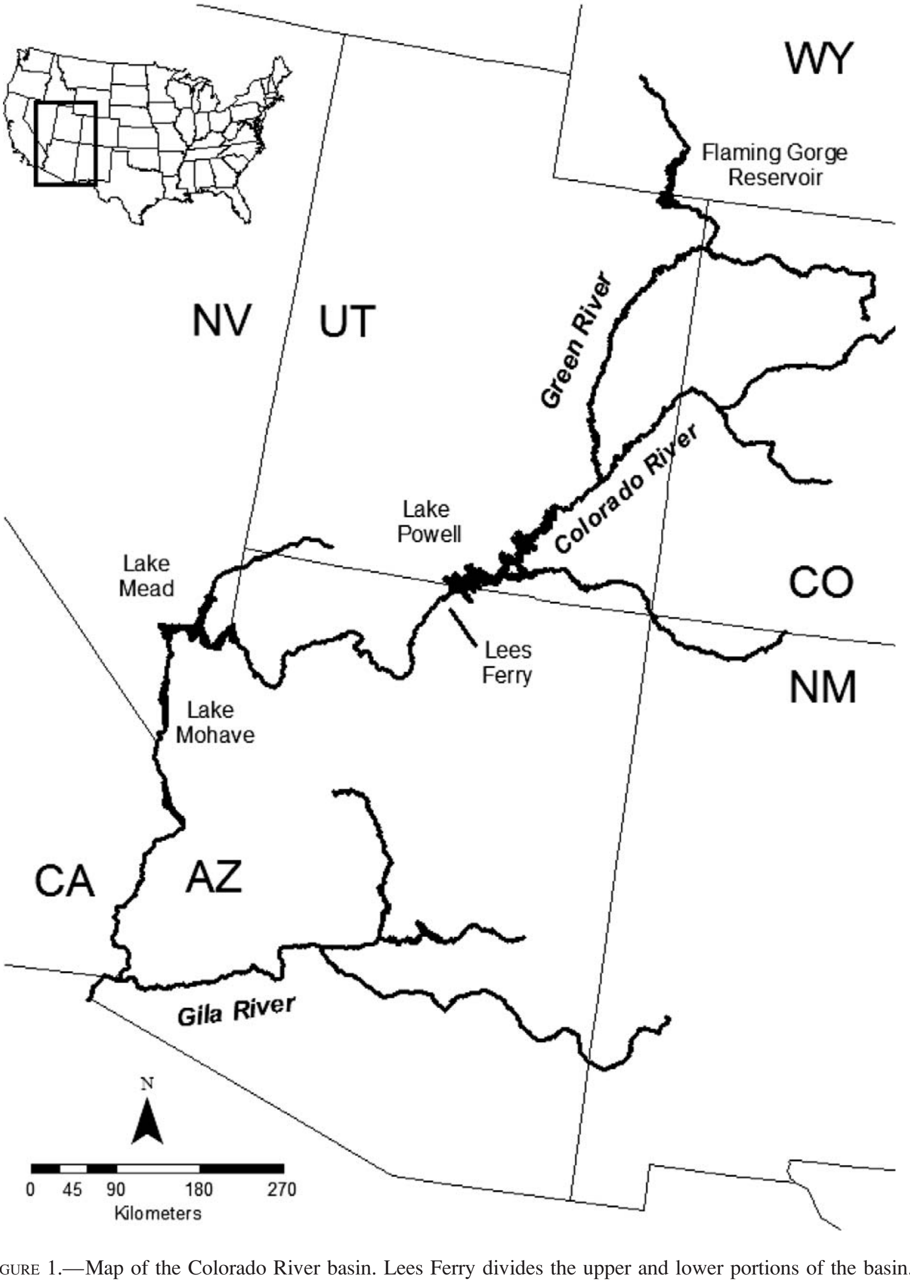

FIGURE 1.—Map of the Colorado River basin. Lees Ferry divides the upper and lower portions of the basin.

recapture probability for each time interval, and parameter estimates are conditional on the model used (Burnham et al. 1987).

Parameters of interest for this study are apparent survival and recapture probability. Apparent survival, φ_j, is the conditional probability of survival in interval j, given that the individual is alive at the beginning of interval j and in the study area available for capture. Thus, $(1 - \varphi)$ represents those animals that die or emigrate. Recapture probability, p_j, is the conditional probability of recapture in year j, given the individual is alive at the beginning of year j. The number of individuals released in year i, R_i, is known and includes releases of newly tagged individuals plus releases of recaptured individuals.

We obtained all data for this study from the

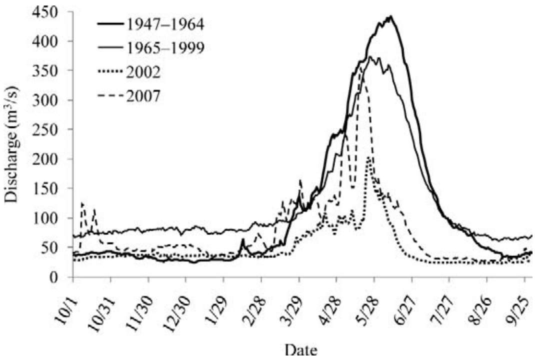

FIGURE 2.—Mean daily discharge of the Green River near Jensen, Utah (U.S. Geological Survey gauge 09261000; unpublished data), for water years 1947–1964 (preimpoundment), 1965–1999 (postimpoundment), and the recent low-flow years 2002 and 2007.

centralized UCRB database, created in Microsoft Access and maintained by U.S. Fish and Wildlife Service (USFWS), Grand Junction, Colorado. The database consisted of two components: hatchery release data from 1995 to 2005 (124,209 records) and recapture data from various field sampling programs through 2006 (4,010 records). Razorback sucker stocking records originated from Ouray National Fish Hatchery (USFWS, Vernal, Utah), Wahweap Warmwater Hatchery (Utah Division of Wildlife Resources [UDWR], Big Water), and Grand Valley Endangered Fish Facility (USFWS, Grand Junction, Colorado). Recapture records resulted from the field sampling efforts of USFWS (Vernal, Utah, and Grand Junction, Colorado), UDWR (Vernal and Moab), Colorado Division of Wildlife (Grand Junction), and Larval Fish Laboratory (Fort Collins, Colorado). Database fields for inclusion in analyses were selected based on factors that may affect survival or recapture probability of hatchery-reared razorback suckers, or both, including: fish TL and weight at time of stocking, year, season, and river reach of stocking, year of recapture, hatchery of origin, and sampling effort.

Fish TL at stocking was reported in the database for individuals, as an average of a stocked batch of fish, or not at all. When lengths were reported for only a portion of a batch of stocked razorback suckers and all other stocking information (year-class, lot number, date) was identical among records for that batch, we calculated the mean of reported lengths and assigned it to remaining records for that batch. Those individuals with no reported TL and not part of a batch from which mean TL could be obtained were eliminated from analysis. The potential importance of fish TL as an individual covariate in analyses was determined to be an acceptable tradeoff for the exclusion of the relatively few records (2.6%) without length information. Razorback suckers that were assigned mean batch lengths and those that were eliminated from analysis were presumed to be representative of the entire data set.

Stocking-season individual covariates were obtained from the months when stocking occurred and were defined as spring (March through May), summer (June through August), autumn (September and October), and winter (November and December). There were no records of fish being stocked in January or February. Designation of seasons was based on objective assessments of prevailing water temperatures: moderate in spring and autumn, warm in summer, and cold in winter.

Anticipating that comparisons of survival and recapture rates among razorback suckers stocked at various locations would be of interest, we used previous studies (Osmundson and Burnham 1998; Osmundson et al. 1998; Bestgen et al. 2007) and information about river gradient, geomorphology, and placement of diversions to divide the UCRB into seven river reaches (Figure 3) into which all stocking records would be arranged. Of those, five reaches received stocked fish on at least one occasion during the study period and became the groups used for parameter comparisons: CO2 (Colorado River upstream of Westwater Canyon to Price-Stubb diversion, plus Gunnison River downstream of Redlands diversion), CO3 (Colorado River from Price–Stubb diversion upstream to Rifle, Colorado), GU2 (Gunnison River upstream of Redlands diversion), GR1 (Green River from Colorado River to downstream end of Desolation–Gray Canyon), and GR3 (Green River upstream of Desolation–Gray Canyon to downstream end of Whirlpool Canyon).

Razorback sucker recaptures originated from multiple agencies conducting research and monitoring throughout the UCRB. Boat and raft electrofishing were the primary sampling methods; however, fyke and trammel nets were employed for several projects. Annual sampling effort within each reach was defined at three levels: (1) at least two of the following occurring in the same year: multipass Colorado pikeminnow *Ptychocheilus lucius* abundance estimate sampling (CS), multipass nonnative fish removal sampling (NNF), and sampling targeting razorback suckers (RZ); (2) either CS or NNF or RZ sampling, in addition to any other less intense sampling; (3) any less intense sampling that did not include CS, NNF, or RZ sampling. Sampling locations, dates, frequencies, and gear for all studies were considered when assigning effort levels.

Similar covariates were eliminated to reduce con-

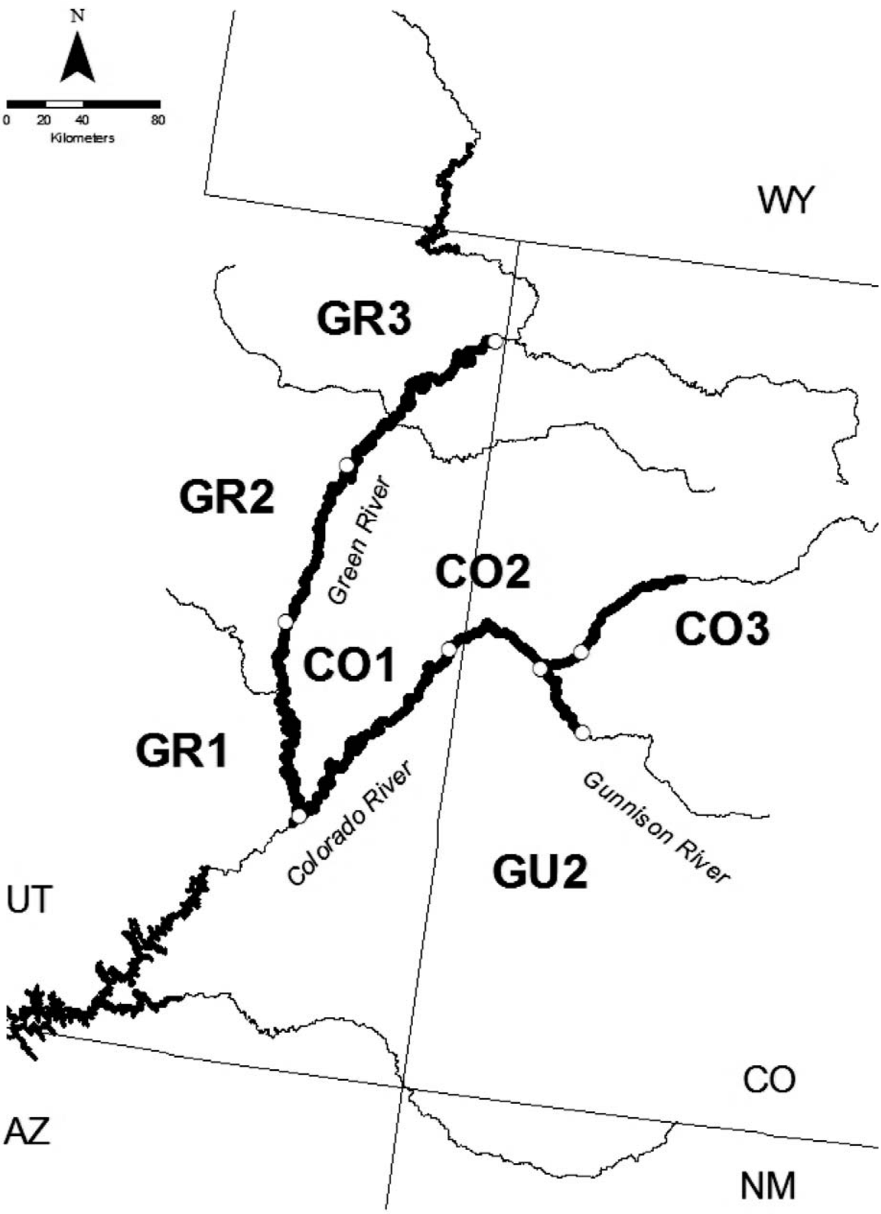

FIGURE 3.—Study reaches within the upper Colorado River basin: CO1 = Colorado River, river kilometer (rkm) 0.0–200.0; CO2 = Colorado River, rkm 200.1–303.2, plus Gunnison River, rkm 0.0–4.9; CO3 = Colorado River, rkm 303.3–390.0; GU2 = Gunnison River, rkm 5.0 or higher; GR1 = Green River, rkm 0.0–206.0; GR2 = Green River, rkm 206.1–347.7; and GR3 = Green River, rkm 347.8–540.0. Open circles denote reach boundaries.

founding. For example, measures of fish length and weight provide redundant information (Beckman 1948; McAda and Wydoski 1980; Didenko et al. 2004), and the effects of each could not be separated if both were included in analysis. Moreover, only 12% of all records of razorback suckers stocked through 2005 contained fish weight data. Therefore, weight was eliminated as a covariate. Hatcheries that stocked fish during the study period included Ouray National Fish Hatchery, Wahweap Warmwater Hatchery, and Grand Valley Endangered Fish Facility. Hatcheries were generally assigned to stock a particular river or reach, such that all reaches, except GR1, were stocked by a single hatchery. Therefore, river reach may act as a surrogate covariate for (and may be confounded with) hatchery. Reach GR1 was stocked with razorback suckers from both the Grand Valley Endangered Fish Facility and Ouray National Fish Hatchery. Stocking year could supply information relating to any annual variation (environmental conditions, hatchery circumstances, or sampling variation). Stocking season provides information about environmental conditions that may vary seasonally, such as discharge, water temperature, and habitat availability at time of stocking. Such environmental data were not in the database and would not only be time-consuming to obtain, but may be confounded with season if added as covariates. Thus, we determined that stocking season as defined was a suitable surrogate for other seasonally varying, but potentially confounded, covariates.

We constructed razorback sucker encounter histories by building a Microsoft Access query that returned stocking year and subsequent recapture years for every stocked fish in the hatchery release portion of the database. Capture occasions occurred annually and the time interval between capture occasions for this study was defined as 1 year; thus, captures of all fish within a calendar year (regardless of date) were considered part of a single capture occasion and multiple within-year captures of a single fish were considered only as a single capture. Variable times of stocking and sampling caused the actual length of time intervals between capture occasions to vary among years. Only 13% of razorback suckers encountered in consecutive calendar years were at large for less than 6 months between those encounters. About 71% of consecutive-year encounters bounded intervals of 6–9 months and the remaining 16% spanned 9–18 months. However, regardless of the time at large for newly stocked razorback suckers, captures of individuals that occurred in consecutive calendar years were considered as two separate occasions, even though fish may have been at large for less than 12 months (e.g., stocked in September 2003 and recaptured in May 2004).

Since irregular interval lengths and recapture efforts may violate underlying assumptions of analysis, a robust design (Pollock 1982) employing multiple capture occasions between survival intervals was considered. However, a minimum number of occasions per sampling session could not be met in all years and many of the already limited recapture records would be eliminated, as they would fall outside the study design constraints. The need to retain as many recapture records as possible to contribute to parameter estimation outweighed the aim of strictly meeting assumptions. Furthermore, differential survival as a function of time at large, if present, should become apparent through comparison of seasonal stocking effects.

After preparing the final data set for input, we used the previously identified groups and covariates, as well as additional effects modeled directly within Program MARK, to build an a priori model set (Appendix A in Zelasko 2008). Apparent survival rate, ϕ model structures included the following effects: group, g, (survival rate estimates vary by river reach [CO2, CO3, GU2, GR1, GR3] into which fish were stocked); constant (constant survival-rate estimate for all individuals and intervals across the study period); time variation, t, (each survival interval has a unique survival rate estimate); first river year, ry1, (first-interval survival rate estimates are different from subsequent-interval rates [i.e., for a given interval, fish have a different survival rate if it is their first interval in the river after being stocked than if it is a subsequent interval]; hatchery-reared individuals may lack predator avoidance, current conditioning, or other survival skills); season (first-interval survival rate estimates vary by season [spring, summer, autumn, winter] when fish were stocked); total length at stocking, TL, (first-interval survival rate estimates are [linearly] related to TL at time of stocking; a squared term [TL^2] was added to model the more plausible quadratic relationship of survival changing with increasing TL; a cubic term [TL^3] was added to prevent the survival curve from increasing or decreasing for the longest TLs, because that is not a reasonable expectation).

Recapture probability, p, model structures included the following effects: group, g, (recapture probabilities vary by river reach into which fish were stocked); constant (constant recapture probability for all individuals and occasions across the study period); time variation, t, (each capture occasion has a unique recapture probability); first river year, ry1, (first-occasion recapture probabilities are different from subsequent-occasion probabilities [i.e., for a given capture year, fish have a different recapture probability if it is their first capture occasion in the river after being stocked than if it is a subsequent occasion]; hatchery-reared individuals may be more or less active in new environment due to displacement or disorientation, resulting in higher or lower recapture probabilities); total length at stocking, TL, TL^2, TL^3; effort (recapture probability of fish stocked into a river reach varies by the sampling effort expended in that reach in subsequent years).

For each parameter, effects were modeled individually, additively, and as interactions. Due to the large data set and numerous a priori model structures for each of the φ and p parameters ($n = 47$ and 34, respectively; Appendix A in Zelasko 2008), running

TABLE 1.—Numbers and total lengths (TLs) of razorback suckers stocked in the upper Colorado River basin, 1995–2005, per year and season. Spring = March, April, and May; summer = June, July, and August; autumn = September and October; and winter = November and December.

Season	TL at stocking (mm)		Year of stocking											Season total
	Mean	Range	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
Winter	229	78–520					453	5,234		1,188		1,907	1,606	10,388
Spring	224	75–497						4,509	60	277	7,888	1,259	255	14,248
Summer	280	75–586				233	2,471	3,726	595	2,331	3,214	3,911	9,096	25,577
Autumn	252	84–530	1,221	1,122	2,926	760	4,588	16,581	5,544	7,852	5,262	14,652	8,405	68,913
Unknown													3	3
Year total			1,221	1,122	2,926	993	7,512	30,050	6,199	11,648	16,364	21,729	19,365	119,129

every combination of model structures and relying on model averaging would have required an inordinate amount of computation time. Therefore, a more efficient procedure to run candidate models was employed. A complex additive model, which contained many of the hypothesized influential effects, was chosen. For initial runs, the complex structure for the φ portion of the model remained the same, while the p portion was simplified. The aim of this strategy was to force the more complex φ structure to absorb much of the variance, allowing better estimation of p. Complexity of p structure was gradually increased, using parameter estimates from each previous model as starting values to aid in estimation. Once all a priori model structures for p had been run with the complex φ structure, the p structure from the best model was retained and run with all variations of φ, starting with the simplest structure. We ran all models using the logit link to maintain a monotonic relationship with the continuous individual covariate, TL.

Model selection was conducted with Akaike's information criterion (AIC; Akaike 1973). Models with lower AIC values are considered more parsimonious and closer to the unknown "truth" that produced the data (Burnham and Anderson 2002). The AIC values reported by Program MARK are based on a modified version of the criterion, denoted AIC_c, which adjusts for small sample size bias (Sugiura 1978; Hurvich and Tsai 1989; Burnham and Anderson 2002) and converges with AIC when sample size is large.

We used all available capture information, including multiple within-year captures, to describe movement of stocked razorback suckers. For each tagged fish with any recapture event, we compiled the following data for both stocking and recapture occasions: river, reach, river kilometer (rkm), and date. Distance between locations (hereafter, "minimum distance traveled," since only the start and end points of travel could be known) and time elapsed were calculated for each leg of a fish's movement. Direction of movement for each leg and any transition within a leg among the three subbasins (CO, GU, and GR) or among the GR subbasin and its tributaries (Duchesne, White, and San Rafael rivers) were described.

Results

Data Set Summary

The final data set for parameter estimation consisted of 119,129 records of stocked razorback suckers and 1,388 recapture events. Stocking occurred in the UCRB every year from 1995 through 2005. Numbers of fish stocked per year ranged from 993 in 1998 to 30,050 in 2000. Fish were stocked at least once in each of the four seasons throughout the study period, but most frequently and at the highest numbers (n = 68,913) in autumn (Table 1), followed by summer, spring, and winter, in descending order. Stocking did not occur every year in all reaches (Table 2). Overall, most razorback suckers were stocked into the Colorado River (n = 61,282) and, in particular, in reach CO2 (n = 44,542), followed by GR3 (n = 26,897), GU2 (n = 18,385), CO3 (n = 16,740), and GR1 (n = 12,565). Fish lengths at stocking ranged from 75 to 586 mm TL (Figure 4) with a mean of 252.5 mm TL. Mean lengths of stocked razorback suckers per season ranged from 224 mm TL in spring to 280 mm TL in summer (Table 1). The largest portion (81%) of the smallest fish (0–99 mm TL) was stocked during spring, while the majority of fish in all other length categories were stocked during autumn (Figure 5). Reach GR1 received the largest stocked fish (mean, 296 mm TL; range, 171–464 mm TL) and reach CO3 the smallest (mean, 163 mm TL; range, 77–388 mm TL; Table 2).

Recaptures of stocked razorback suckers occurred on every capture occasion from 1997 through 2006, but not in 1996 (Table 3). Years 2005 and 2006 produced the most recaptures (n = 463 and 428, respectively), as did the Colorado River, in general, and reach CO2 (n = 441, 2000–2006), specifically.

The largest portions of recaptures consisted of fish

TABLE 2.—Numbers and total lengths (TLs) of razorback suckers stocked in five reaches of the upper Colorado River basin, 1995–2005, by year. Reach abbreviations are as follows: CO2 = Colorado River, river kilometer (rkm) 200.1–303.2, plus Gunnison River, rkm 0.0–4.9; CO3 = Colorado River, rkm 303.3–390.0; GU2 = Gunnison River, rkm 5.0 or greater; GR1 = Green River, rkm 0.0–206.0; and GR3 = Green River, rkm 347.8–540.0.

River reach	TL at stocking (mm)		Year of stocking											Reach total
	Mean	Range	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
CO2	263	80–530						11,434	698	10,468	5,505	6,153	10,284	44,542
CO3	163	77–388					3,411	11,810	1,456	52	11			16,740
GU2	217	75–586	316	287	2,926	606	2,744	6,582	4,045	854	25			18,385
GR1	296	171–464									2,377	5,957	4,231	12,565
GR3	294	127–560	905	835		387	1,357	224		274	8,446	9,619	4,850	26,897
Year total			1,221	1,122	2,926	993	7,512	30,050	6,199	11,648	16,364	21,729	19,365	119,129

stocked in 2004 ($n = 412$) or those stocked into reach CO2 ($n = 601$; Table 4). No fish stocked during 1995 were subsequently recaptured. Fish stocked in autumn make up more than 72% of recaptures (n = 1,006), followed by summer ($n = 154$), spring ($n = 113$), winter ($n = 112$); there were three recaptures for which season of stocking was not known. Lengths at stocking for razorback suckers that were subsequently recaptured ranged from 129 to 495 mm TL with a mean of 327 mm TL (Figure 4).

Model Selection

Relatively parameter-rich models that included interactions of group and time effects produced many inestimable parameters and were removed from consideration, resulting in a reduced set of reasonable models. There were more than 50 models in the resulting set (Appendix B in Zelasko 2008), many of the simplest of which were run to provide starting values for more complex a priori models.

The model with the lowest AIC_c value carried nearly 100% of AIC_c weight (Table 5), and the second-best model was about 10 AIC_c points different. The next closest models were closely grouped and all 225 or more AIC_c points from the best model. Therefore, the top-ranked model was chosen for further inference. Goodness-of-fit testing was not possible due to sparse data and inclusion of individual covariates.

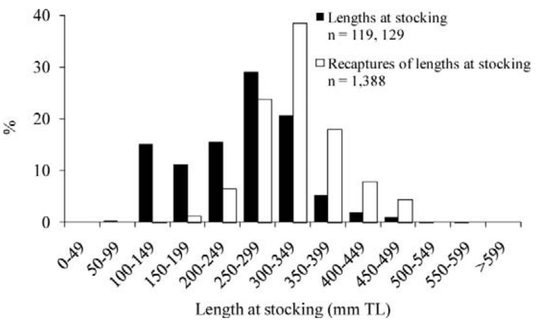

FIGURE 4.—Length frequencies of razorback suckers stocked and subsequently recaptured in the upper Colorado River basin, 1995–2006.

Parameter Estimates

The top-ranked model contained 24 estimable parameters. Survival was modeled with seven parameters: an intercept, first-interval effect, three stocking-season effects, and both linear and quadratic effects of TL. The intercept represented survival through any post-ry1 interval. Parameter values for the function of logit φ were as follows: intercept = 1.0916 (SE = 0.1538), ry1 = −11.9386 (1.0735), winter = 0.0904 (0.1481), spring = −0.1683 (0.1438), summer = −1.5970 (0.1337), TL = 0.0416 (0.0067), and TL^2 = −0.00003 (0.00001). Large negative logit values for effects ry1 and summer indicate lower survival in those times. The model resulted in five survival rate

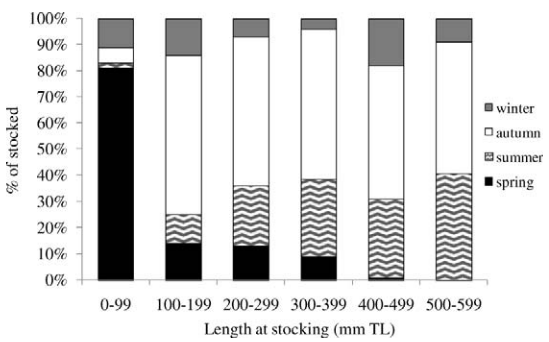

FIGURE 5.—Percentages of razorback suckers stocked into the upper Colorado River basin in spring, summer, autumn, and winter 1995–2005, by length range. Spring = March, April, and May; summer = June, July, and August; autumn = September and October; and winter = November and December;.

TABLE 3.—Numbers of razorback suckers recaptured in the upper Colorado River basin, 1996–2006, by recapture year and reach. Reach abbreviations not given in Table 2 are as follows: CO1 = Colorado River, rkm 0.0–200.0; GR2 = Green River, rkm 206.1–347.7.

Recapture reach	Recapture year											Reach total
	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	
CO1			1		2	1		68	25	175		272
CO2					22	30	3	89	96	186	15	441
CO3												0
GU2		2			3	2			3	1	1	12
GR1				4	2	3	3	1			276	289
GR2				1		5	1	1		10	38	56
GR3		3		26	8	33	16	11	32	91	98	318
Year total	0	5	1	31	37	74	23	170	156	463	428	1,388

estimates, including four first-interval, TL-dependent φ values for fish stocked during each of the stocking seasons and one constant φ for all fish subsequent to their first intervals in the river.

Total length at stocking had a large and positive effect on first-interval survival rates (ry1 φ values) of razorback suckers stocked in the UCRB (Figure 6). Averaging over season of stocking, survival rates of razorback suckers stocked at less than 200 mm TL were near zero but increased to 0.75 or higher for the few fish larger than 500 mm TL. Survival rate for razorback suckers stocked at the average length of 252.5 mm TL was low: only 0.05 (95% confidence interval [CI], 0.042–0.071). For razorback suckers less than about 500 mm TL, first-interval survival rate estimates averaged over stocking season were lower than the constant, subsequent-interval estimate, but increased as length at stocking increased. In fact, 95% CIs for first-interval and subsequent-interval estimates did not overlap until TL at stocking reached 415 mm.

Season of stocking also had a large effect on first-interval survival of razorback suckers. Survival patterns over a range of lengths at stocking were similar for fish stocked in spring, autumn, and winter (Figure 7). However, survival was comparatively much lower for fish of all sizes when stocked in summer. For example, ry1 survival rate for razorback suckers of average length (252.5 mm TL) stocked in summer was less than 0.02 (95% CI, 0.012–0.022), but was 0.07 (CI, 0.044–0.094), 0.08 (CI, 0.057–0.100), and 0.08 (CI, 0.057–0.118) for fish of the same length stocked in spring, autumn, and winter, respectively. As would be expected with additive models, the same pattern was observed for fish stocked at the currently recommended length of 300 mm TL and even 400 mm TL (Figure 8). Survival rate estimate CIs for razorback suckers stocked in summer did not begin to overlap with those of any other season until length at stocking reached approximately 450 mm TL.

Overall survival rate for razorback suckers through any interval subsequent to their first intervals in the river (post-ry1 φ), was estimated at 0.75 (95% CI, 0.688–0.801). The post-ry1 survival rate was independent of fish length at stocking and stocking season.

In the 24-parameter top model, recapture probability was modeled with 17 parameters: an intercept, four group parameters, 10 occasions (1996 was inestimable, see below), first-occasion effect, and both linear and quadratic effects of TL. The intercept represented the fifth group on the 11th occasion. Parameter estimates for the function of logit p (Table 6) produced 105 recapture probability estimates, including 11 time-varying, first-occasion, TL-dependent p values and 10 time-varying, subsequent-occasion p values for each of the five river reaches where fish were stocked. Since no fish stocked in 1995 were recaptured, the 1996

TABLE 4.—Numbers of razorback suckers recaptured in the upper Colorado River basin, 1996–2006, by stocking reach and year. No fish stocked in 1995 were subsequently recaptured. See Table 2 for reach definitions.

Stocking reach	Year of stocking										Reach total
	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
CO2					55	7	253	50	228	8	601
CO3				10	7	6					23
GU2	21	4	3	18	5	29	25				105
GR1								5	80	168	253
GR3	3		61	30	29		2	91	104	86	406
Year total	24	4	64	58	96	42	280	146	412	262	1,388

TABLE 5.—Cormack–Jolly–Seber open-population models used to estimate apparent survival (φ) and recapture probability (p) for hatchery-reared razorback suckers stocked into the upper Colorado River basin from 1995 to 2005. The top eight models (selected by Akaike's information criterion adjusted for small sample size bias (AIC_c) are shown for comparison. Other abbreviations are as follows: ΔAIC_c = the AIC_c of the model in question less that of the model with the minimum AIC_c; AIC_c weight = the support for the model in question relative to the entire set of candidate models; model likelihood = ratio of AIC_c weight to that of the model with the minimum AIC_c; K = number of parameters; and deviance = −2 • log-likelihood of the model in question less −2 • log-likelihood of the saturated model (the model with as many parameters as degrees of freedom). Effects included stocking season, group or stocking reach (g), time (t), first interval or occasion in the river (ry1), and total length at stocking (TL and TL^2).

Model	AIC_c	ΔAIC_c	AIC_c weight	Model likelihood	K	Deviance
{φ(ryl + season + TL + TL^2)p(g + ryl + TL + TL^2 + t])}	15,614.58	0.00	0.99	1.00	24	15,566.58
{φ(ryl + season + TL + TL^2)p(g + t)}	15,624.88	10.30	0.01	0.01	21	15,582.88
{φ(ryl + TL + TL^2)p(g + [ryl + TL + TL^2 + t])}	15,839.80	225.22	0.00	0.00	21	15,797.80
{φ(g + [ryl + TL + TL^2])p(g + [ryl + TL + TL^2 + t])}	15,843.27	228.69	0.00	0.00	25	15,793.27
{φ(ryl + TL + TL^2)p(g + [ryl + t])}	15,844.07	229.49	0.00	0.00	19	15,806.07
{φ(g + [ryl + TL + TL^2])p(g + [ryl + t])}	15,845.24	230.66	0.00	0.00	23	15,799.24
{φ(g + [ryl + TL + TL^2])p(g + t)}	15,850.34	235.76	0.00	0.00	22	15,806.34
{φ(ryl + TL + TL^2)p(g + t)}	15,845.29	239.70	0.00	0.00	18	15,818.29

recapture probability was inestimable for all five groups, which reduced the number of estimates of p to 100.

Recapture probability estimates were all relatively low, ranging from 0.002 to 0.128 for razorback suckers of average length at stocking (Table 7). Razorback suckers stocked into reach GR1 produced the highest p values, followed by those in CO2, GR3, CO3, and GU2, in descending order. Although first-occasion (ry1) recapture probability estimates were higher than subsequent-occasion (post-ry1) estimates for razorback suckers of average length at stocking, the estimates did not differ for any capture occasion within any group, based on overlapping 95% CIs. However, recapture probabilities (ry1 or post-ry1) differed among several occasions within each group. Confidence limits for 1998 and 2002 estimates, in particular, overlapped with those of very few other years. Among groups, differences were only detected between groups GR1 and GU2 on occasions 2001 and 2003–2006 (both ry1 and post-ry1) and between CO2 and GU2 in 2005 and 2006 for post-ry1 occasions only. The parameter estimate for total length at stocking (0.0106, 95% CI, –0.0023–0.0237) suggested that TL had a small positive effect on recapture probabilities. For example, first-interval recapture probabilities for fish stocked into reach CO2, which fell between the extremes overall, increased an average of 0.014 (range, 0.001–0.027; Figure 9) when the size of stocked fish increased from the mean length of 252.5 to 400 mm TL. While that translates to a 25% increase, the effect is minor due

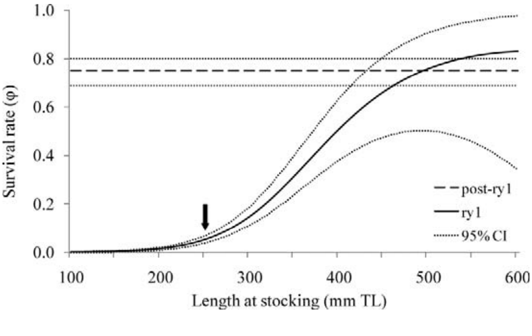

FIGURE 6.—Estimates of first-interval (ry1) and subsequent-interval (post-ry1) survival rates and 95% confidence intervals (CIs) averaged over stocking season for razorback suckers stocked into the upper Colorado River basin, 1995–2005. The arrow indicates the first-interval survival rate estimate for a razorback sucker of average total length at stocking (252.5 mm).

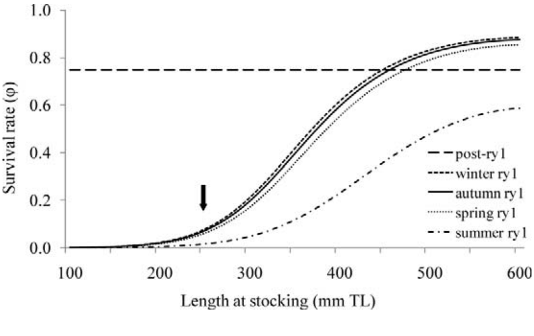

FIGURE 7.—Estimates of first-interval (ry1) survival rates per stocking season compared with subsequent-interval (post-ry1) rates for razorback suckers stocked into the upper Colorado River basin, 1995–2005. See Figure 5 for definitions of seasons. The arrow indicates the first-interval survival rate estimate for a razorback sucker of average total length at stocking (252.5 mm).

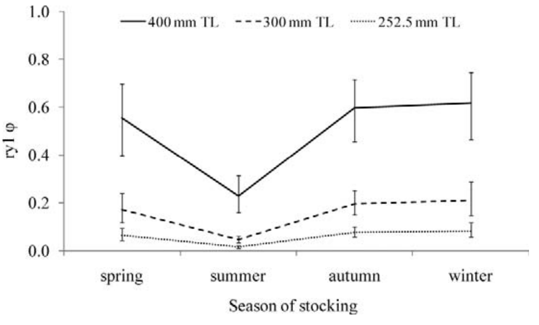

FIGURE 8.—Predicted first-interval survival rate (ry1 φ) estimates for razorback suckers of 252.5, 300, and 400 mm total length (TL) stocked into the upper Colorado River basin during spring, summer, autumn, and winter (see Figure 5) 1995–2005; 252.5 mm was the average length at stocking, 300 mm the recommended length at stocking (Nesler et al. 2003), and 400 mm the length of an adult razorback sucker.

to the extremely low recapture probabilities estimated overall.

Movement

There were 150,121 records of stocked razorback suckers and 2,839 records of recapture events available to analyze movement patterns from 1995 through 2006. Of the recapture events, 2,747 contained information on both minimum distances traveled and time elapsed since stocking or previous recapture. Distance, time, and rates of razorback sucker movements varied widely over the study period, but mean values were all highest for initial legs (stocking to first capture event) than subsequent legs (Table 8). Mean minimum distance traveled by a razorback sucker on any leg was 54.7 km (range, 0–514.9 km). The greatest minimum distance traveled (514.9 km) was produced by a fish moving from reach GR3 to CO1 over 410 d (rate = 1.25 km/d). The 294-mm-TL razorback sucker was stocked in the Green River at rkm 514.1 (downstream from Split Mountain) in April 2003 and recaptured (the only time during this study period) in the Colorado River at rkm 0.8 in May 2004 when it measured 390 mm TL. Only about 15% of minimum distances exceeded 100 km and only 1.5% exceeded 300 km. Mean time elapsed from a recapture event (or stocking) to next recapture event was 254 d (range, 0–3,164 d). The maximum time elapsed (3,164 d = 8.8 years) resulted from a 362-mm-TL razorback sucker stocked during October 1996 in the Gunnison River (rkm 91.8) and recaptured in June 2005 in the Colorado River (rkm 213.0), a difference of 153 km. It measured 490 mm TL upon recapture. The mean rate of movement for all legs traveled by all razorback suckers was 0.87 km/d (range, 0–55.37 km/d). Mean minimum distance traveled, time elapsed, and rate of travel per fish (from stocking to last recapture) were 60.0 km, 278 d, and 0.91 km/d, respectively.

Of the 2,752 recapture events where direction of movement from the previous capture (or stocking) was known, 2,552 legs (92.7%) consisted entirely of, or were initiated as, downstream movements. In fact, 96.3% of initial-leg movements were downstream, as were the majority of subsequent legs (56.5–66.7%). Only 3.4% of initial-leg movements for razorback suckers were in an upstream direction, while subsequent legs were upstream 0–23.2% of the time. The remaining 0.3% of initial-leg movements and 20.4–33.3% of subsequent-leg movements were recaptures of razorback suckers at the same locations as their previous captures, resulting in no known direction of movement.

Within any of the three main-stem rivers (CO, GU, GR), mean downstream distance moved was 52.9 km, while mean upstream distance moved was 22.9 km. Travel among all three rivers within a leg produced the longest mean distance traveled, 454.6 km. Travel in a leg involving a tributary produced a mean distance of 186.3 km and resulted from fish that originated in a Green River tributary (Duchesne, White, or San Rafael River), moved down to the main channel, and proceeded to any downstream Green River reach (GR3, GR2, or GR1).

Movement of razorback suckers out of their initial stocking reaches was more frequent in the Colorado

TABLE 6.—Parameter estimates and SEs for the function of logit *p*, the recapture probability for hatchery-reared razorback suckers stocked into the upper Colorado River basin from 1995 to 2005. See Table 2 for reach definitions. Variable ry1 = the effect of first occasion in the river (versus subsequent occasions). The intercept represents group GR3 in capture year 2006. The recapture probability for 1996 was inestimable because no fish stocked in 1995 were recaptured in 1996.

Variable	Estimate	SE
Intercept	−3.35726	0.16400
CO2	0.21519	0.07833
CO3	−0.37224	0.24873
GU2	−0.49808	0.13690
GR1	0.38577	0.09873
1997	−0.22120	0.47129
1998	−2.42192	1.01031
1999	0.45963	0.20758
2000	0.55527	0.19381
2001	0.88734	0.15524
2002	−0.60358	0.22961
2003	0.35296	0.10738
2004	−0.15033	0.10187
2005	0.32576	0.07312
ryl	−1.65113	1.14833
TL	0.01069	0.00663
TL^2	−0.00001	0.00001

TABLE 7.—First-occasion (ry1) and subsequent-occasion (post-ry1) probabilities of recapture (p) and 95% confidence intervals (CIs) for a razorback sucker of average total length (252.5 mm) stocked into five reaches of the upper Colorado River basin (see Table 2), 1995–2005. Recapture probabilities for 1996 were inestimable because no fish stocked in 1995 were recaptured in 1996.

Recapture year	CO2		CO3		GU2		GR1		GR3	
	p	95% CI	p	95% CI	p	95% CI	p	95% CI	p	95% CI
ry1										
1997	0.039	0.015–0.097	0.022	0.008–0.062	0.020	0.008–0.049	0.046	0.018–0.115	0.032	0.012–0.080
1998	0.005	0.001–0.032	0.003	0.000–0.019	0.002	0.000–0.016	0.005	0.001–0.039	0.004	0.000–0.026
1999	0.075	0.046–0.119	0.043	0.022–0.081	0.038	0.023–0.062	0.087	0.053–0.141	0.061	0.038–0.098
2000	0.082	0.052–0.126	0.047	0.025–0.086	0.042	0.026–0.066	0.095	0.060–0.148	0.067	0.043–0.103
2001	0.110	0.078–0.154	0.064	0.037–0.109	0.057	0.039–0.084	0.128	0.088–0.183	0.091	0.063–0.129
2002	0.027	0.016–0.045	0.015	0.008–0.029	0.013	0.008–0.023	0.032	0.019–0.055	0.022	0.013–0.037
2003	0.068	0.048–0.094	0.039	0.022–0.067	0.034	0.023–0.051	0.079	0.054–0.114	0.055	0.038–0.079
2004	0.042	0.030–0.059	0.024	0.013–0.042	0.021	0.014–0.032	0.049	0.034–0.072	0.034	0.024–0.049
2005	0.066	0.048–0.090	0.038	0.022–0.065	0.033	0.022–0.050	0.077	0.055–0.108	0.054	0.038–0.075
2006	0.049	0.035–0.067	0.028	0.016–0.048	0.024	0.016–0.036	0.057	0.040–0.080	0.039	0.028–0.055
post-ry1										
1997	0.033	0.013–0.083	0.019	0.007–0.052	0.017	0.007–0.042	0.039	0.015–0.098	0.027	0.011–0.068
1998	0.004	0.001–0.027	0.002	0.000–0.016	0.002	0.000–0.013	0.005	0.001–0.033	0.003	0.000–0.022
1999	0.064	0.041–0.100	0.037	0.019–0.068	0.032	0.020–0.051	0.075	0.047–0.119	0.052	0.033–0.082
2000	0.070	0.045–0.107	0.040	0.022–0.073	0.036	0.022–0.056	0.082	0.052–0.127	0.057	0.037–0.088
2001	0.095	0.066–0.135	0.055	0.032–0.095	0.049	0.032–0.073	0.111	0.075–0.161	0.078	0.053–0.113
2002	0.023	0.014–0.038	0.013	0.007–0.025	0.011	0.007–0.019	0.027	0.016–0.046	0.019	0.011–0.031
2003	0.058	0.042–0.079	0.033	0.019–0.057	0.029	0.020–0.043	0.068	0.047–0.097	0.047	0.033–0.067
2004	0.036	0.026–0.049	0.020	0.012–0.035	0.018	0.012–0.027	0.042	0.029–0.060	0.029	0.060–0.041
2005	0.056	0.042–0.076	0.032	0.019–0.055	0.028	0.019–0.042	0.066	0.048–0.091	0.046	0.033–0.063
2006	0.041	0.031–0.055	0.023	0.014–0.040	0.021	0.014–0.030	0.049	0.036–0.066	0.034	0.025–0.046

and Gunnison River subbasins than in the Green River subbasin (Table 9). Only 7.7% (range, 2.9–10.3%) of fish stocked into Green River reaches and subsequently recaptured were ever recaptured outside of their original stocking reaches, compared with 36.9% (range, 30.1–100%) of those stocked into the Colorado or Gunnison rivers and later recaptured outside of their stocking reaches.

Movement frequencies out of reaches CO3 and GU2, in particular, were very high. All recaptures of razorback suckers stocked into reach CO3 occurred in downstream reaches CO2 or CO1, and nearly half of the recaptures of those stocked into reach GU2 were in the next downstream reach, CO2. Otherwise, most recaptures occurred in the same reaches into which fish were stocked or the next downstream reaches, respectively. Razorback suckers stocked into reach CO2 and subsequently recaptured remained there (including movements into the mouth of the Gunnison River up to Redlands diversion), moved downstream into CO1, or moved down to CO1 then upstream into GR1. Those stocked into GU2 and later recaptured remained there, moved down to CO2 or CO1, or moved down then upstream into GR1. Fish stocked into GR3 remained in the reach (including the Duchesne and White rivers), moved downstream into reaches GR2 or GR1 (including the San Rafael River), or moved either above or below the confluence with the Colorado River to reach CO1. Those stocked into GR1 remained, moved upstream into GR2, or moved downstream to either above or below the confluence with the Colorado River into reach CO1.

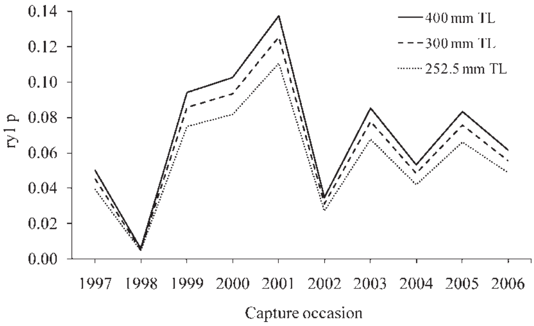

FIGURE 9.—Predicted first-occasion recapture probability estimates (ry1 p) for razorback suckers of 252.5, 300, and 400 mm TL stocked into reach CO2 (see Figure 3), 1997–2006. The recapture probability for 1996 was inestimable because no fish stocked in 1995 were recaptured in 1996.

Razorback suckers stocked during winter moved the longest distances on average (86.7 km) for any leg of travel, but those stocked in summer moved at the highest rates on average (1.34 km/d; Table 10). Mean initial-leg rates of travel were generally higher for razorback suckers stocked at smaller sizes (Figure 10). Fish less than 300 mm TL at time of stocking traveled

TABLE 8.—Mean minimum distance traveled, time elapsed, and rate of travel per leg of movements made by stocked razorback suckers in the upper Colorado River basin, 1995–2006.

		Distance (km)			Time (d)			Rate (km/d)		
Leg	*n*	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Stocking to capture 1	2,501	58.9	0	514.9	262	0	3,164	0.93	0	55.37
Capture 1 to capture 2	215	11.5	0	194.2	179	1	1,799	0.44	0	8.50
Capture 2 to capture 3	28	9.4	0	44.5	103	1	1171	0.67	0	11.80
Capture 3 to capture 4	3	11.9	0	30.4	133	1	279	0.05	0	0.11

at a mean rate of 1.3 km/d on initial legs of travel, while those at least 300 mm TL traveled at a mean rate of 0.6 km/d. We considered investigation of variation in annual, initial-leg movements relative to environmental effects (discharge, water temperature) and stocking protocols (density). However, we dismissed that analysis because of multiple confounding factors, including substantial movement out of certain reaches and imbalance of numbers of razorback suckers stocked across seasons, reaches, and years.

Discussion

Evaluation of stocking programs designed to enhance populations of depleted fishes is an essential part of a well-informed adaptive management process. Our analysis of a large and long-term tag-recapture data set for razorback suckers stocked in the upper Colorado River basin suggested low first-year survival. Further, survival was positively related to fish length at stocking, but only modest for fish of average length, and was particularly low in summer. Survival of stocked fish after their first interval in the river was higher than during their first interval. Downstream movement rates of stocked razorback suckers was high, particularly just after stocking. In the following sections we discuss these findings in more detail and recommend changes in stocking protocols that may improve survival of stocked fish and increase prospects for recovery of razorback suckers.

First-Interval and Subsequent-Interval Survival

Survival rates of stocked razorback suckers through their first intervals in the river were lower than subsequent intervals for fish of nearly all lengths at stocking. Low first-year survival of hatchery-reared razorback suckers has been previously demonstrated for fish stocked into both river and reservoir environments, and was thought to be due mostly to predation by nonnative fishes (Marsh and Brooks 1989; Marsh et al. 2005). High postrelease 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 native fishes. For example, white sturgeon *Acipenser transmontanus* stocked into the Kootenai River, Idaho, exhibited mean first-year survival rates that were 30–40% lower than in subsequent years (Ireland et al. 2002; Justice et al. 2009). Hatchery-reared bonytail *Gila elegans*, a Colorado River basin endangered species, had such low return rates after being at large for more than 6 months that poststocking survival was

TABLE 9.—Movements of hatchery-reared razorback suckers from their stocking reaches to subsequent recapture reaches (see Tables 2, 3) in the upper Colorado River basin. Percentages of total movements from the initial reach are given in parentheses. Abbreviations not defined previously are as follows: SR = San Rafael River (tributary of the Green River that joins it at rkm 156.2); DU = Duchesne River (tributary of the Green River that joins it at rkm 399.3); and WH = White River (tributary of the Green River that joins it at rkm 396.7).

	Recapture reach										
Stocking reach	CO3	CO2	CO1	GU3	GR3	GR2	GR1	DU	WH	SR	Total
CO3		27 (87)	4 (13)								31
CO2	650 (70)	278 (30)					2 (<1)				930
CO1											
GU2		97 (45)	18 (8)	92 (43)			7 (3)				214
GR3			2 (<1)		1245 (90)	74 (5)	43 (3)	14 (1)	9 ()	1 (<1)	1,388
GR2											
GR1			6 (2)			2 (1)	268 (97)				276
DU											
WH											
SR											
Total		774	308	92	1245	76	320	14	9	1	2,839

TABLE 10.—Mean minimum distance traveled (km) and rate of travel (km/d) between captures for razorback suckers stocked in spring, summer, autumn, and winter (see Table 1) in the upper Colorado River basin, 1995–2006.

	Spring		Summer		Autumn		Winter	
Leg	Distance	Rate	Distance	Rate	Distance	Rate	Distance	Rate
Stocking to capture 1	53.5	1.24	40.1	1.29	65.4	0.61	95.5	0.37
Capture 1 to capture 2	7.8	0.46	14.9	2.00	14.5	0.34	10.4	0.96
Capture 2 to capture 3	2.5	0.21	2.1	0.30	16.9	1.45	27.5	0.45
Capture 3 to capture 4	0.0	0.00			17.8	0.08		
Overall	48.9	1.16	38.3	1.34	61.0	0.59	86.7	0.42

assumed to be extremely low (Badame and Hudson 2003; Bestgen et al. 2008). Low first-year survival rates of stocked hatchery fish were perhaps not surprising, given the relatively benign environment (stable or no flow velocity, constant temperatures, dependable and abundant food, predator-free habitats) in which fish were raised (Suboski and Templeton 1989; Olla et al. 1998).

The survival rate for stocked razorback suckers after the first interval was more encouraging, as hatchery-reared individuals survived at rates similar to their wild counterparts. The estimated survival rate for any stocked razorback sucker through any interval subsequent to its first in the river was 0.75, a rate similar to that assumed in the integrated stocking plan for age-4 (adult) fish (0.70) and that estimated for wild fish in the Green River (0.71–0.76) from 1980 to 1999 (Modde et al. 1996; Bestgen et al. 2002; Nesler et al. 2003). High subsequent-interval survival rates, observations of stocked razorback suckers in spawning aggregations with wild individuals (Modde et al. 2005), and annual production of larvae in the Green River since 2000, presumably from stocked fish (K. Bestgen, unpublished), suggested that hatchery-reared fish were acclimating to the riverine environment and may contribute to recovery if recruitment bottlenecks can be overcome.

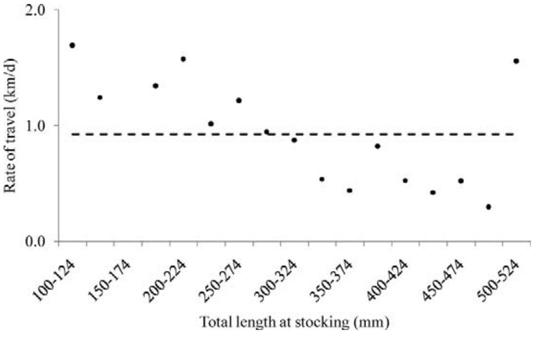

FIGURE 10.—Mean initial-leg rates of travel for razorback suckers stocked and recaptured in the upper Colorado River basin, 1995–2006. The dashed line represents the mean rate of travel for razorback suckers of all lengths at stocking. The mean rates of travel for fish stocked at 150–174 mm (9.7 km/d [off the graph]) and 500–524 mm (1.6 km/d) were calculated with only one and two data points, respectively.

Even though passive integrated transponder (PIT) tag loss was assumed to be low for this study, especially compared with the Carlin tags that were used from 1980 to 1992 (Prentice et al. 1990; McAllister et al. 1992; Ombredane et al. 1998; Ward and David 2006), faulty scanning equipment, lack of scanning, and data-recording errors may cause virtual tag loss and, potentially, biased estimates of survival (Bestgen et al. 2002). Of the 4,010 total razorback sucker capture events we examined, at least 275 records (6.9%) had PIT tag errors which made them unusable. Another 328 capture records (8.2%) did not have associated stocking data, which could be the result of captures of wild untagged fish, captures of hatchery-reared untagged fish, loss of tags, failure of equipment to detect tags, or failure to scan fish prior to stocking. Accurate tagging, tag detection, and data recording are minimal requirements to understand provenance of captured fish (hatchery or wild) and recruitment rates of razorback suckers.

Investigations have begun to address underlying causes of high poststocking mortality in razorback suckers (Marsh et al. 2005; this study). For example, exercise conditioning was found to increase swim performances of razorback suckers by 26% (Ward and Hilwig 2004) and may reduce downstream displacement to unsuitable habitats. Combined predator exposure and exercise conditioning showed promising results for razorback sucker survival: treatment fish (exercised and exposed to predation) experienced significantly lower mortality (31 ± 4.41% [mean ± SE]) in the presence of flathead catfish *Pylodictis olivaris* than did unexercised, predator-naïve fish (46 ± 4.88%) (Mueller et al. 2007). Treatment and control fish were tested together, however, allowing for social learning between the groups, the effect of which could not be quantified. Consequently, the higher mortality rate for control fish was conservative compared with a truly naïve group, unable to learn from more predator-

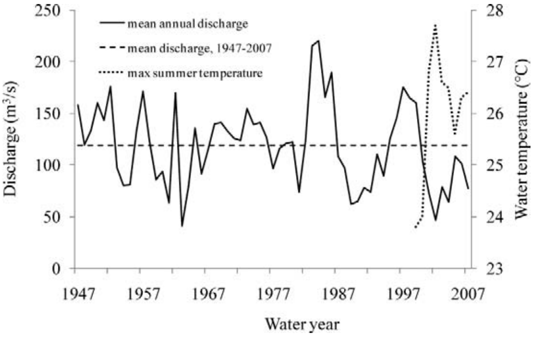

FIGURE 11.—Mean annual discharge for individual water years and the entire period 1947–2007 and maximum summer water temperatures from 1 June through 31 August 1999–2007 in the Green River near Jensen, Utah (U.S. Geological Survey gauge 09261000, unpublished data).

savvy conspecifics. Exposure to chemical cues of a predator (pike odor and trout skin extract with alarm signal) successfully induced antipredator behavior in rainbow trout *Oncorhynchus mykiss* and may be useful to develop antipredator behavior in razorback suckers (Brown and Smith 1998; Olla et al. 1998). Predator-avoidance training and additional conditioning of hatchery-reared razorback suckers, including use of outdoor grow-out ponds, may increase low first-interval survival.

Length at Stocking and First-Interval Survival

Total length at stocking was also a strong influence on first-interval survival of stocked razorback suckers and managers should continue to stock as large a fish as possible to increase survival. First-year survival rates estimated for repatriated razorback suckers in Lake Mohave were slightly lower than those in this study for fish up to 400 mm TL: 300 and 350 mm TL stocked fish survived at rates of 0.10 and 0.26, respectively, in Lake Mohave (Marsh et al. 2005) versus 0.15 and 0.31, respectively, in this study, averaged across season of stocking. Fish stocked at 400 mm TL survived first intervals at similar rates in both studies, and those larger than 400 mm TL survived at slightly higher rates in Lake Mohave than in this study: 500 mm TL razorback suckers had a predicted survival rate greater than 0.90 in Lake Mohave (Figure 1 in Marsh et al. 2005) versus 0.76 in this study. Overall, however, predicted TL-dependent survival curves were similar and showed higher survival for larger fish. While TL undoubtedly continued to affect razorback sucker survival in subsequent intervals, we did not model that effect because lengths were not available for all of the relatively few recaptured fish. We did, however, allow TL at stocking to influence all subsequent survival intervals, but those models fell well below models in which TL only affected first intervals (Appendix B in Zelasko 2008). The importance of fish length to explain survival rates underscores the need to collect length information on hatchery-reared razorback suckers prior to stocking.

We note that survival rates of razorback suckers assumed in management plans are overestimated for all ages (and, therefore, TLs) at stocking (Nesler et al. 2003). For example, fish stocked at age 2 (approximately 300 mm TL) were assumed to survive at a rate of 0.50, while our analysis predicted survival 60–90% lower, at 0.05–0.21, depending on stocking season. Even adult fish ($\geq$age 4 and 400 mm TL) did not survive at the assumed 0.70 rate during their first interval, but instead rates were 0.23–0.62. Growing larger razorback suckers in the hatchery would increase first-interval survival, but would require more space, food, and time. A cost : benefit analysis would be necessary to quantify the trade-offs regarding optimum fish size at stocking (Heidinger 1993).

Stocking Season and First-Interval Survival

Stocking season greatly affected first-interval survival of razorback suckers: summer-stocked fish (June, July, or August) had the lowest survival rates, while all other seasons had higher and similar survival rates. A concern with analyzing survival by season of stocking was that razorback suckers stocked earlier in a year may have been susceptible to causes of mortality for a longer period of time than those stocked later. Following that logic, one would expect more distinct seasonal survival rate curves, with the lowest survival rates being predicted for fish stocked in spring, followed by summer, autumn, and winter, in ascending order. However, our results showed tight grouping of spring, autumn, and winter first-interval survival curves (Figure 7) and confidence limits of the survival rate estimate for summer-stocked razorback suckers that did not overlap those of any other stocking season. We were also suspicious that season and TL might be confounded (i.e., the smallest fish may have been stocked during summer) since the model used to calculate seasonal survival rate estimates also included length at stocking. On the contrary, the largest razorback suckers, on average, were stocked in summer (mean = 280 mm TL, range = 75–586 mm TL, Table 1), and fish released in spring accounted for more than 81% of the smallest fish stocked in the study (<100 mm TL, Figure 5). We concluded, therefore, that the effect of summer stocking was valid and not confounded with TL.

While naturally warm summer water temperatures are beneficial to growth and survival of both larval and adult razorback suckers (Clarkson and Childs 2000; Bestgen 2008), those temperatures may adversely affect survival of stocked individuals. High water temperatures in summer months, which often exceed 25°C in middle Green River near Jensen, Utah (Figure 11), may debilitate fish already stressed from handling and transport. Increased stress, in turn, leaves fish more susceptible to common aquatic parasites and diseases (Post 1983). For instance, bonytail released in June 2005 and recaptured in the Green River 2–4 months later all had fungal or *Lernea* sp. infections, or both (Bestgen et al. 2008). Furthermore, several predaceous species introduced into the UCRB, such as centrarchids and ictalurids, are more active in warm water than in cold water. In the Gila River, Arizona, ictalurid catfish predation on razorback suckers stocked in winter, when the predators were feeding less frequently, was a fraction of that on razorback suckers stocked in summer (Marsh and Brooks 1989). Considering the extremely low survival rates of razorback suckers stocked in summer, releases during those months ought to be avoided until evidence suggests summer stocking is advantageous. Furthermore, the cost : benefit analysis to determine optimal size of stocked razorback suckers should include a seasonal component, which would allow individual hatcheries with unique operational constraints to adjust production strategies accordingly.

Reach, Time, and Survival

Neither stocking reach nor year appreciably affected survival rate estimates of stocked razorback suckers. Disparity among numbers of fish stocked and movement among reaches after stocking may have attenuated any differences in survival stemming from geomorphology of the reaches or hatchery origin of the fish. However, the stocking reach effect on survival should be investigated in future analyses. As stocking protocols become more consistent, and only reaches which retain reasonable numbers of fish are included in analyses, estimation of razorback sucker survival rates per reach should be attainable.

Stocking year is certainly important to the survival of stocked fish. Low flows associated with drought years beginning around year 2000 may have reduced available habitat for stocked razorback suckers, resulting in crowding, increased disease transmission, and increased encounters with native and nonnative predators (Bestgen et al. 2007). However, the imbalance of stocking and recapture data impeded detection of time-varying survival on an annual scale. For example, while stocking occurred in every year of the study, numbers of razorback suckers stocked ranged from fewer than 1,000 to more than 30,000. Furthermore, fish were not stocked into every reach in every year (Table 2), making investigations of interactive effects among reaches and years impossible. A better understanding of effects of stocking reaches and years on survival could be obtained if a more balanced data set, such as that generated through continued implementation of the integrated stocking plan, was available. Such analyses would aid in evaluating reach-specific flow recommendations or predator removal actions and assist with evaluating if subbasin recovery goal criteria, including population size and trends (e.g., population rates of change), were being met.

Apparent Survival versus True Survival

Apparent survival (φ) differs from true survival (S) 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 available for capture in the study area. Thus, $1 - \varphi$ represents the probability that individuals either die or emigrate to areas where they are not susceptible to capture. In this study, apparent survival closely approximated true survival because most fish were susceptible to capture. Sampling covered most of the UCRB and very few fish were ever encountered in less-sampled canyon-bound reaches of the Colorado River downstream from its confluence with the Green River, including the inflow area of Lake Powell.

Recapture Probability

Recapture probability, p, was not the primary parameter of interest in this study but is inextricably linked to survival estimation in the following manner:

$$\log_e \mathrm{L}(\varphi, p|\mathrm{EH}) = \sum(\text{number of animals}) \times \log_e[\text{probability}(\mathrm{EH})],$$

which states that the log-likelihood of the parameters, given the encounter histories (EH) observed, is equal to the summation of the product of the number of animals that share an encounter history and the log of the probability of that encounter history. The probability of an encounter history is the product of an animal's survival rates and recapture probabilities (or 1 − recapture probabilities, if not recaptured) for all intervals and occasions. Higher recapture probabilities result in more precise survival estimates (Lebreton et al. 1992), so it is worthwhile to design studies with that in mind.

First-Occasion and Subsequent-Occasion Recapture Probability

For any given capture occasion (sampling year), recapture probability was slightly higher for razorback suckers of average length at stocking when it was their first capture occasion after stocking than if it was a subsequent capture occasion (Table 7). Overall, both probabilities were low: the highest achieved for average-sized stocked razorback suckers was 0.13. In mark–recapture studies, one aims to capture most individuals from a released cohort on the first occasion after initial marking (stocking), which equates to high recapture probability. This study did not always accomplish that aim because data were collected from a variety of sampling programs where effort was sometimes low after stocking of substantial numbers of fish, and very few efforts specifically targeted stocked razorback suckers. In contrast, species-specific, Colorado pikeminnow abundance-estimate sampling produced recapture probabilities ranging from 0.01 to 0.20 in the Green River subbasin in 2000–2003 (Bestgen et al. 2007), and 0.07–0.19 in the Colorado River subbasin in 1991–1994 (Osmundson and Burnham 1998). Future recapture probability estimations would be aided by more consistent sampling efforts targeted specifically at razorback suckers, particularly in years when intensive sampling, for studies such as Colorado pikeminnow abundance estimation, is not occurring. Not only might recapture probabilities increase, but a uniform protocol would better meet the underlying assumption that recaptures are made within brief time periods relative to intervals between tagging.

Length at Stocking and First-Occasion Recapture Probability

The parameter estimate for total length at stocking was not different from the model's intercept (i.e., the 95% CI for the TL beta estimate overlapped zero), although larger stocked razorback suckers had slightly higher recapture probabilities than smaller ones. Because length generally affects recapture probability of fishes (Anderson 1995; Bestgen et al. 2007; Dauwalter and Fisher 2007; Korman et al. 2009), we retained the first-occasion TL effect in the p structure of the model. More notable was that razorback suckers stocked at larger sizes were recaptured in higher proportions than average-sized fish (Figure 4), regardless of capture occasion. For instance, fish stocked from 250 to 299 mm TL accounted for 29.1% of all fish stocked, while only 23.7% of recaptures consisted of fish stocked in that size range. Conversely, fish 300–349 mm TL comprised 20.6% of the total stocked, but made up 38.5% of all recaptures. Fish in larger length categories followed the same trend, with even larger increases in recapture percentages. Similar length-related results have been reported for return rates of bonytail (Badame and Hudson 2003) and razorback suckers (Burdick 2003) in the UCRB. Much of the data for this study was collected by boat electrofishing, a method efficient for sampling large rivers and known to immobilize larger fish more effectively than smaller ones (Dolan and Miranda 2003; Snyder 2003), so it was not surprising that fish stocked at larger sizes had higher recapture probabilities. We also demonstrated that larger razorback suckers survived at higher rates, which possibly contributed to higher recapture probabilities as size at stocking increased. Higher recapture probabilities would be an additional benefit of stocking larger razorback suckers and should be considered when weighing the costs and benefits of increasing lengths of stocked fish.

Reach, Time, and Recapture Probability

Other factors that affected recapture probabilities were stocking reach (group, g) and capture occasion (time, t). Modeling interactions of the variables did not produce estimable parameters, probably as a result of the data imbalance across stocking reaches and years discussed earlier. The additive effect of the factors, however, was retained in the top model. Overall, razorback suckers stocked into reach GR1 had the highest recapture probabilities, followed by those stocked into reaches CO2, GR3, CO3, and GU2, in descending order (Table 7). We note that recapture probabilities per group refer to fish stocked into particular reaches, not recaptured in those reaches. Razorback suckers were most often recaptured in the reach into which they were stocked (Table 9), but enough were found elsewhere that the distinction becomes important. However, addition of reach covariates or a multistate analysis (e.g., Bestgen et al. 2007) was not warranted, because data were too sparse to estimate those effects. Therefore, we proceeded with recapture probabilities referring solely to fish stocked into particular reaches, regardless of where they were recaptured.

There were only a few differences among recapture probabilities produced by all additive group and time combinations, but enough to keep both factors in the top model. The differences reflect inherent sampling heterogeneity produced over a long study period and by unequal sampling efforts, as well as the aforementioned data imbalance (namely, large differences in number of fish stocked per reach and year). We attempted to simplify estimation by categorizing the 11 years of sampling effort in each stocking reach into three levels, but the model may not have been complex enough to account for the heterogeneity and ranked low among all models. Furthermore, effort expended in a reach did not always relate directly to recapture probabilities of fish stocked into that reach, as many fish were captured elsewhere. For example, fish

TABLE 11.—Mean minimum distance traveled, time elapsed, and rate of travel from stocking to first recapture of razorback suckers stocked into reaches of varying lengths (see Table 2) in the upper Colorado River basin, 1995–2006.

Stocking reach	Reach length (km)	Mean distance (km)	Mean time (d)	Mean rate (km/d)
CO2	103	46	299	0.44
CO3	87	113	666	1.06
GU2	92	95	465	2.17
GR1	192	64	335	0.31
GR3	206	60	180	1.19

stocked into reach CO3 had some of the lowest *p* values, and one might conclude that limited sampling through the years was responsible. However, all recaptures of razorback suckers stocked into CO3 occurred in the more heavily sampled downstream reaches CO2 and CO1. Similarly, fish stocked into GU2 had the lowest *p* values and the reach experienced the least sampling. However, almost half the recaptures of fish stocked into GU2 occurred in reach CO2. Since models including effort effects did not produce constructive results, they were not considered further.

Sampling heterogeneity, fluctuating stocking numbers, and environmental factors may all contribute to annual variation among *p* values. For example, recapture probabilities for 1996 were inestimable for razorback suckers stocked in all reaches, because no fish stocked during 1995 were recaptured. Recapture probabilities in 1998 were the lowest of all estimable years, although sampling in that year occurred in nearly all reaches and included razorback sucker monitoring in the Green River subbasin and intensive Colorado pikeminnow abundance-estimate sampling in the Colorado River subbasin. The low *p* values in 1998 were due, in part, to limited stocking of razorback suckers in 1995–1997: approximately 1,000–3,000 fish per year into only one or two reaches (GU2 and GR3, Table 2). Recapture probabilities increased steadily from 1999 through 2001, but declined again in 2002 when no sampling occurred in the Colorado and Gunnison River subbasins. Another explanation for low 2002 recapture probabilities was low flows in that drought year: mean flow of the Green River at Jensen, Utah, was the second-lowest reported since 1947 (Figure 11). Low flows impeded sampling with boat and raft by making certain habitat types that typically hold fish inaccessible or unavailable (e.g., backwaters), and reduced flow certainly reduced the length of the usual sampling season. Associated high water temperatures may have caused fish to remain more sedentary or occupy deeper, pool habitats, or both, making them less susceptible to capture.

Movement

Distance, time, and rate.—The longest distances traveled per leg, most time elapsed between legs, and highest rates of travel per leg occurred during initial legs of all razorback sucker movements, implying that most movement occurred between stocking and first recapture event. This may have been due to razorback suckers exploring their new environment, seeking suitable habitat, or simply getting displaced by current. All three measures of movement declined by 28–95% on subsequent legs, presumably after most displacement subsided, fish found preferred habitats, or initial mortality occurred.

Direction.—Most movements, regardless of leg, were in a downstream direction. It is unknown whether downstream movements were active intentional movements to preferred habitat or passive displacement (Marsh and Brooks 1989; Mueller et al. 2003). Razorback suckers stocked into upstream, higher gradient, or canyon reaches, such as CO3, may actively seek downstream, lower gradient, slow-water reaches, such as CO2. Those preferences are supported by the species' life history (McAda and Wydoski 1980; Minckley et al. 1991) and movement data collected in this study. However, fish reared in a hatchery may simply not be able to negotiate river current when experiencing it for the first time and get swept downstream (Ward and Hilwig 2004), regardless of reach geomorphology.

Reach.—Insufficient fish movements among reaches precluded a multistate analysis, which would have estimated the probabilities of razorback suckers moving from one reach to another. Some movement differences among reaches, nevertheless, were noteworthy. Movements of razorback suckers out of their initial stocking reaches were more frequent in the Colorado and Gunnison River subbasins than in the Green River subbasin. Reaches that experienced the highest percentages of departures happened to be the shortest stocking reaches in the study area: reaches CO2, CO3, and GU2 were about 103, 87, and 92 km in length, respectively, while GR1 and GR3 were 192 and 206 km long, respectively. Logically, movements of similar distances would result in the crossing of reach boundaries more often in shorter reaches than in longer ones. However, initial-leg movements were longest, on average, for razorback suckers stocked into the two shortest reaches (Table 11), which were nearly twice as long as those for fish stocked into other reaches. Therefore, movement out of reaches CO2, CO3, and GU2 may not have been more frequent due to reach length alone. Fish in the two shortest reaches, CO3 and GU2, also showed high initial-leg rates of travel. Movements out of those higher-gradient reaches were always in a downstream direction, so causation (active departure or passive displacement) cannot be determined. Since there were few or no significant differences in survival and recapture probabilities of razorback suckers stocked into various reaches, and the species' stocking plan predicted mixing of individuals among subbasins, movement out of certain reaches may not be a major concern for managers. However, the cost-effectiveness of stocking large numbers of hatchery-reared razorback suckers into reaches from which a large percentage of fish leave should be assessed.

Stocking season and total length.—Razorback suckers stocked during winter traveled the longest distances on average, and those stocked during summer traveled at the highest rates on average. Both seasons are characterized by water temperatures at the extremes of the range for streams in the basin, probably requiring razorback suckers to seek habitat of adequate depth for protection. Furthermore, snowmelt runoff in late spring to early summer results in high flows that could displace stocked razorback suckers farther downstream than lower flows in other seasons.

Mean initial-leg rates of travel were higher for razorback suckers stocked at smaller sizes (Figure 10). Rates were approximately two times higher for fish less than 300 mm TL than for those 300 mm TL or longer, suggesting that smaller fish may be displaced more easily than larger ones. Whether such displacement was active or passive, the consequences may include lower survival for smaller-sized razorback suckers, as observed in this study.

In summary, razorback sucker recovery depends on a complex set of management actions including habitat restoration, provision of adequate flow and temperature conditions, reduction of negative effects of nonnative species, and stocking of hatchery-reared individuals, each of which contributes to the underlying goal of self-sustaining populations required for delisting the species (Bestgen 1990; USFWS 2002). This study provides managers with accurate survival rate estimates for stocked fish and factors that influenced those estimates, essential tools used to evaluate hatchery production strategies and stocking protocols. These results should immediately advance recovery prospects for the razorback sucker in the upper Colorado River basin.

Acknowledgments

This study was funded by the Recovery Implementation Program for Endangered Fish Species in the upper Colorado River basin. The program is a joint effort of the USFWS, the U.S. Bureau of Reclamation (USBR), the Western Area Power Administration, the states of Colorado, Utah, and Wyoming, upper basin water users, environmental organizations, the Colorado River Energy Distributors Association, and the National Park Service. This study originated from K. Zelasko's thesis, in partial fulfillment of the requirements for the degree of Master of Science, Colorado State University. 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, J. Frantz, T. Czapla, A. Kantola, and R. Muth. C. McAda, and T. Francis (USFWS, Grand Junction, Colorado) maintain the database from which all razorback sucker stocking and recapture data were obtained. Data were supplied to the database by countless individuals and multiple agencies over many years. Razorback sucker stocking records originated from Ouray National Fish Hatchery (USFWS, Vernal, Utah), Wahweap Warmwater Hatchery (UDWR, Big Water, Utah), and Grand Valley Endangered Fish Facility (USFWS, Grand Junction, Colorado). Recapture records resulted from the field sampling efforts of USFWS (Vernal, Utah, and Grand Junction, Colorado), UDWR (Vernal and Moab, Utah), Colorado Division of Wildlife (Grand Junction, Colorado), and LFL (Fort Collins, Colorado). The reviews by P. Doherty, C. McAda, M. Trammel, T. Czapla, and others are greatly appreciated.

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