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THESIS

SURVIVAL RATE ESTIMATION AND MOVEMENT OF HATCHERY-REARED RAZORBACK SUCKERS *XYRAUCHEN TEXANUS* IN THE UPPER COLORADO RIVER BASIN, UTAH AND COLORADO

Submitted by
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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY KOREEN ZELASKO ENTITLED SURVIVAL RATE ESTIMATION AND MOVEMENT OF HATCHERY-REARED RAZORBACK SUCKERS *XYRAUCHEN TEXANUS* IN THE UPPER COLORADO RIVER BASIN, UTAH AND COLORADO BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

SURVIVAL RATE ESTIMATION AND MOVEMENT OF HATCHERY-REARED RAZORBACK SUCKERS *XYRAUCHEN TEXANUS* IN THE UPPER COLORADO RIVER BASIN, UTAH AND COLORADO

Status and trajectory of an animal population depends on its demographic rates, and endangered species management, in particular, relies on such quantifiable population descriptors to guide the recovery process. Recovery goals 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. Current wild populations are so depleted that the first management action to achieve recovery is to reestablish populations with hatchery-produced fish. Stocking goals call for 9,930 age-2 (≥ 300 mm TL) individuals to be stocked in each of the middle Green River and upper Colorado River subbasins for each of six consecutive years, thus creating the presumptive recovery populations. The plan assumes annual survival rates of 50% for age-2 fish, 60% for age-3 fish, and 70% for adult (≥ age-4) fish.

The scope of this study is restricted to 7 reaches in the Green and Colorado River subbasins of the Upper Colorado River Basin, which are delineated by differing river gradients and geomorphology: CO1 (Colorado River from confluence with Green River to upstream end of Westwater Canyon, RK 0.0 – 200.0), CO2 (Colorado River from upstream of Westwater Canyon to Price-Stubb diversion, RK 200.1 – 303.2; plus Gunnison River downstream of Redlands diversion, RK 0.0 – 4.9), CO3 (Colorado River from Price-Stubb diversion upstream to Rifle, RK 303.3 – 390.0), GU2 (Gunnison River upstream of Redlands diversion, >RK 4.9), GR1 (Green River from Colorado River to just downstream of Desolation-Gray Canyon, RK 0.0 – 206.0), GR2 (Green River, Desolation-Gray Canyon, RK 206.1 – 347.7), and GR3 (Green River from upstream end of Desolation-Gray Canyon to mouth of Whirlpool Canyon, RK 347.8 – 540.0). Only reaches CO2, CO3, GU2, GR1, and GR3 received stocked fish on at least one occasion during the study period.

A total of 119,129 individually PIT-tagged razorback suckers were stocked into the Colorado, Gunnison, and Green rivers from 1995 through 2005. Recapture frequencies among years (subsequent to stocking years) ranged from 0 – 4. Parameters of interest for this study were apparent survival, φ, and capture probability, p. Covariates obtained from stocking or capture information that may affect annual φ or p included: river, river reach, year, season, and individual fish total length (TL). Other effects investigated included 1st year in the river (ry1) versus subsequent years (post-ry1), for both φ and p, and annual sampling effort expended in river reaches, for p only. A 1st-year effect was included to determine if survival and/or capture probability of newly stocked fish was different than in subsequent years. A set of a priori candidate models was created based on available data and biology of the razorback sucker and was analyzed with Program MARK. Akaike's Information Criterion model selection procedure was used to choose best model structure(s) for the data, from which maximum likelihood estimates of apparent survival, capture probability, and precision were obtained. Recapture data, including multiple within-year captures, were also used to describe post-stocking movement of razorback suckers. Distance traveled, time elapsed, and direction of movement between recaptures were recorded for each leg of a fish's movement.

Total length at stocking had a large and positive effect on 1st-interval (ry1) survival rates of razorback suckers stocked in the Upper Colorado River Basin. Averaging over season of stocking, ry1 survival rates of razorback suckers stocked at <200 mm TL approached 0 but increased to 0.75 or higher for the few fish >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). As length at stocking increased, 1st-interval survival rate estimates averaged over stocking season increased. Season of stocking also had a large effect on 1st-interval survival of razorback suckers. Predicted 1st-interval survival rate for average length razorback suckers stocked in summer was <0.02 (95% CI: 0.012 – 0.022), but was 0.08 (0.057 – 0.100), 0.08 (0.057 – 0.118), and 0.07 (0.044 – 0.094) for fish of the same length stocked in autumn, winter, and spring, respectively. The same pattern was observed for fish stocked at the currently recommended length of 300 mm TL and even 400 mm TL, which suggested a large effect of season on survival, regardless of fish size. Overall survival rate for razorback suckers through any interval subsequent to their first interval in the river (post-ry1) was estimated at 0.75 (95% CI: 0.688 – 0.801) and was independent of fish length at stocking and stocking season. That rate is similar to 0.70 assumed in the integrated stocking plan for adult (≥ age-4) fish and agrees with survival rates estimated for wild adult razorback suckers in the middle Green River. Capture probability estimates were all relatively low, ranging from 0.002 – 0.128 for razorback suckers of average length at stocking. Razorback suckers stocked into reach GR1 produced the highest *p*'s, followed by CO2, GR3, CO3, and GU2, in descending order. Although 1st-occasion (ry1) capture probability estimates were higher than subsequent-occasion (post-ry1) estimates, the two estimates did not differ for any capture occasion within any group, based on overlapping 95% CIs. The parameter estimate for total length at stocking (0.0106, 95% CI: −0.0023 – 0.0237) did not differ significantly from the intercept, suggesting that TL had little effect on capture probabilities.

Mean distance traveled in river kilometers (RK), time elapsed in days (d), and rate of travel (RK/d) by a razorback sucker on any leg of movement (from one recapture event, or stocking, to next recapture event) were 54.7 RK (range: 0 – 514.9), 254 days (range: 0 – 3,164), and 0.87 RK/d (range: 0 – 55.37), respectively, and were all highest

for initial legs (stocking to first capture event) than subsequent legs. Razorback suckers stocked during winter moved the longest distances on average (86.7 RK), but those stocked in summer moved at the highest rates on average (1.34 RK/d). There was no discernible pattern in mean distances traveled by fish stocked at sizes >150 mm TL, but fish smaller than that moved <20 RK over 13 or fewer days on average. Nearly all (92.7%) movements were in a downstream direction. Most recaptures occurred in the same reaches into which fish were stocked or the next downstream reaches, respectively. Movement of razorback suckers out of their initial stocking reaches was more frequent in the Colorado and Gunnison River subbasins (36.9%, range: 30.1 – 100%) than in the Green River subbasin (7.7%, range: 2.9 – 10.3%).

Maintenance of self-sustaining populations is the underlying goal of all razorback sucker recovery efforts. My results suggest that stocking fish larger than the currently recommended 300 mm TL in seasons other than summer would aid in accomplishing that goal. A cost:benefit analysis of hatchery production and stocking strategies is necessary to determine the trade-offs of raising fewer, larger razorback suckers with higher survival rates versus many, smaller fish with lower survival. Techniques to improve 1st-interval survival, including exercise conditioning, predator-avoidance training, and pond rearing, should be investigated further. Implementation of management strategies derived from these post-stocking survival rate estimates and movement results will immediately enhance recovery prospects for razorback sucker in the Upper Colorado River Basin.

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Chuck McAda and Travis Francis (USFWS, Grand Junction, Colorado) maintain the database from which I obtained all razorback sucker stocking and recapture data for this project. They deserve acknowledgement for that alone, but also for enduring dozens of my emails over several months to rectify discrepancies. I appreciate their patience and know that the razorback sucker dataset is better for it. 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 (Utah Division of Wildlife Resources (UDWR), Big Water, Utah), and 24-Road Fish Hatchery (USFWS, Grand Junction, Colorado). Recapture records resulted from the field sampling efforts of

USFWS (Vernal, Utah, and Grand Junction, Colorado), UDWR (Vernal, Utah, and Moab, Utah), Colorado Division of Wildlife (Grand Junction, Colorado), and LFL (Fort Collins, Colorado). I recognize the contribution of each of those efforts to this study.

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For Ma,

who supported my education, in every way

For Dad,

who instilled in me the values of nature

For Bobby,

who motivated this endeavor

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Introduction

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 desert Southwest supports several endangered species that are currently the focus of recovery efforts. One of these species, razorback sucker *Xyrauchen texanus* (Abbott), family Catostomidae, has experienced dramatic declines in distribution and abundance resulting largely from anthropogenic modifications to the basin. Natural populations of the species are now rare. Recovery of razorback sucker requires several management actions, including stocking of hatchery-reared individuals. Survival rates for wild razorback suckers have been defined by previous studies, but were unknown for naïve hatchery fish. In this study, I estimated survival rates for hatchery-reared razorback suckers from multiple years of mark-recapture data. First, I present background on the species to put the findings in perspective.

Distribution and status

Razorback sucker is a catostomid endemic to the Colorado River Basin (Figure 1, Minckley et al. 1991). Early observers found them widespread and abundant 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). Decline of razorback sucker coincided with multiple anthropogenic alterations to habitat and biota within the basin. Dam construction and non-native species introductions are considered the most detrimental, leaving only small, fragmented populations. Between 1980 and 2000 in the Upper Colorado River Basin (UCRB), razorback suckers were captured sporadically on the Green, Yampa, and San Juan rivers, Utah, Colorado, and New Mexico; most were concentrated in the middle portion of the Green River, between Duchesne and Yampa rivers. However, wild fish are rare and may have since been extirpated in the UCRB (Bestgen 1990, Bestgen et al. 2002). In the Lower Colorado River Basin downstream of Glen Canyon Dam, individuals are found primarily in Lake Mohave and Lake Mead, Arizona and Nevada. However, the once large population in Lake Mohave was last estimated to number fewer than 3,000 fish (Marsh et al. 2003).

Declines in distribution and abundance of razorback sucker resulted in its listing 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 outline specific criteria required for downlisting and delisting the species, including self-sustaining population sizes for razorback sucker in each portion of the Colorado River Basin. At the time recovery goals were written, populations were deemed so imperiled that the first management action listed toward achieving recovery was "Reestablish populations with hatchery-produced fish" (U.S. Fish and Wildlife Service 2002). However, before stocking can be effectively used as a recovery tool, life history of the target species and hatchery-produced individuals must be better understood.

Life history

Razorback sucker is a "big river," long-lived catostomid, historically reaching 1 m in length and weighing up to 6 kg (Minckley 1983, Bestgen et al. 2002). Otolith-aging indicated that some of the largest fish may be 24 – 44 years old (McCarthy and Minckley

1987). Razorback suckers reach reproductive maturity at approximately 4 years of age and >400 mm total length (TL).

Upstream spawning movements, sometimes 100 km in length or more, occur in spring in the UCRB to two known locations: lower Yampa River near its confluence with the Green River and middle Green River between RK 492 and 501 (Tyus and Karp 1990). Spawning occurs from late March to early June on the ascending limb of the hydrograph, in water temperatures from 6 – 19°C (McAda and Wydoski 1980, Tyus and Karp 1990, Snyder and Muth 2004). Aggregations of razorback suckers have been observed over cobble/gravel bars located on or adjacent to riffles in water with velocities <1 m/s and depths usually <1 m (McAda and Wydoski 1980, Wick et al. 1982, Tyus and Karp 1990, Minckley et al. 1991, Snyder and Muth 2004). Egg hatching is limited at temperatures <10°C, and is most successful between 10 and 20°C (Marsh 1985, Bozek et al. 1990, Snyder and Muth 2004). Time of swim-up from spawning gravel is 4 – 21 days and proportional to temperature (Marsh 1985, Snyder and Muth 2004), after which larvae drift downstream to low-velocity floodplain or backwater nursery habitat (McAda and Wydoski 1980, Minckley et al. 1991). Growth of larvae is also proportional to water temperature and highest at 25.5 C, the highest temperature tested (Clarkson and Childs 2000, Bestgen 2008).

Adult razorback suckers require deeper, low-velocity habitat in spring and winter, but have been known to occupy shallow sandbars in summer (McAda and Wydoski 1980). Long gill rakers, sub-terminal mouth position, and diet all support the species' propensity for backwater-type habitats or reservoirs (Minckley et al. 1991).

Decline

Although larvae have been captured in the Upper Colorado River Basin 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 range (Minckley 1983, Tyus 1987, Marsh and Minckley 1989).

Suspected biotic and abiotic mechanisms driving reduced recruitment and decline are hypothesized to occur in every life stage and have been partially summarized in a conceptual model (Figure 2, Bestgen et al. 2007b). Low numbers of reproducing adults, impediments to spawning migrations, reduced flows and temperatures downstream of dams, and egg-predation by non-native 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 non-native species influence survival of early life stages (Tyus 1987, Minckley et al. 1991, Mueller et al. 2003, Bestgen 2008). These factors, singly or interacting, are thought to inhibit most recruitment to the juvenile life stage (Holden et al. 2000).

Recovery plan

The U. S. Fish and Wildlife Service (2002) requires that each of the Upper and Lower Colorado River basins maintains 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 population is required for the Green River subbasin and the other is to occur in either the upper Colorado River subbasin or the San Juan River subbasin, and abundance of adults in each population 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. The UCRB recovery effort is partitioned into two recovery programs: (1) the Upper Colorado River Endangered Fish Recovery Program (UCRRP), which includes the Green and Colorado River subbasins, and (2) the San Juan River Recovery Implementation Program (SJRRIP). Each cooperative program includes multiple management strategies addressing habitat, instream flow, and nonnative species. However, without recruitment, protection of remnant adult populations and associated habitat would not be sufficient to prevent extinction of razorback sucker. Therefore, it is recognized that the required self-sustaining populations can only be achieved with the aid of hatchery augmentation (U.S. Fish and Wildlife Service 2002).

In response to the recovery goals and the need to evaluate success of stocked fish in 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 Upper Basin plan lists razorback sucker as the first priority over Colorado pikeminnow (*Ptychocheilus lucius* Girard) and bonytail (*Gila elegans* Baird and Girard); defines the age of an adult as 4+ years; recommends maintaining a minimum of four adult age classes; and assumes survival rates of 50% for age-2 fish, 60% for age-3 fish, and 70% for adult fish. The assumed adult survival rate for stocked fish is consistent with that for wild individuals, which was estimated at 71% and 73% by Modde et al. (1996) and Bestgen et al. (2002), respectively. Stocking goals call for 9,930 age-2 (≥ 300 mm TL) individuals to be stocked in each of the middle Green River and upper Colorado River subbasins in six consecutive years, creating two presumed adult populations of 7,546 suckers in year 6. The difference between this population size and that in the recovery goals (5,800 individuals) is a buffer to account for additional adult mortality. The same procedure will be followed in the lower Green River subbasin to produce a third, redundant population in case of a catastrophic event (Nesler et al. 2003).

A fundamental requirement of any recovery action is evaluation. Reviews of the Upper Colorado River Basin endangered fish stocking plans began in the late 1990's. One study followed 45 stocked and radio-tagged razorback suckers (450 – 550 mm TL) for approximately 1.5 years (Burdick and Bonar 1997), at the end of which, 6 fish remained alive, 4 were confirmed dead, and fates of the other 35 were unknown. Another study evaluated the "survival and performance" of several size classes of stocked razorback suckers through recapture data (Burdick 2003). Nearly 50,000 fish were stocked from 1994 to 2000, fish were recaptured from 1997 to 2001, and recapture rates were reported. Only 84 (0.2%) razorback suckers were recaptured after being at large ≥ 6 months after stocking. A more recent overview of the stocking program summarizes stocking and capture records throughout the basin from 1995 to 2005 (Francis and McAda 2006). Previously, an insufficient number of stocked razorback sucker recaptures prohibited evaluation of the recovery goal survival rate assumption – a key, but uncertain, element. To date, many razorback suckers have been stocked and recaptured in the Upper Colorado River Basin, and data may be sufficient for a robust analysis.

Justification and objectives

The purpose of this study is to provide a comprehensive, basin-wide assessment of certain assumptions and demographic parameters for razorback sucker recovery goals in the UCRB.

The objectives of this study are to:

1. compile and proof stocking and capture data for razorback suckers stocked into the Upper Colorado River Basin,
2. identify possible strata and/or covariates for data analysis,

3. analyze data with appropriate parameter estimation software to obtain the most unbiased and precise survival rate estimates possible,
4. compare survival rate estimates to those assumed in the integrated stocking plan to determine if stocking goals are being met,
5. analyze movement of stocked razorback suckers to identify patterns that may affect stocking protocol, and
6. recommend revisions to integrated stocking plan, based on results of analyses.

Results will be useful to managers attempting to restore razorback sucker in the UCRB and may also guide future production and stocking strategies for hatcheries.

Methods

Study area

The Upper Colorado River Basin covers portions of Wyoming, Utah, Colorado, New Mexico, and Arizona (Figure 3). The basin is bordered by the Rocky Mountains on the east and various ranges to the west, including the Wasatch Mountains. 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. 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 reaches. 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 1964 completion of Flaming Gorge Dam, located on the upper Green River, Utah, spring peak flows are lower and summer base flows are higher than historic levels. Recent low flow years have resulted in spring peaks with reduced duration and magnitude (Figure 4), a factor that may affect reproduction and recruitment of several UCRB endangered fish, including razorback sucker. 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).

Parameter estimation

Data proofing.—I obtained all data for this study from the centralized Upper Colorado River Basin Database, created in Microsoft Access and maintained by USFWS in Grand Junction, Colorado. The database consisted of two components: hatchery release data through 2005 (124,209 records) and capture data from field sampling programs through 2006 (4,010 records). The hatchery release data fields included: hatchery agency and source, unique Passive Integrated Transponder (PIT) tag number per fish, length (mm TL), weight (g), year class, lot number, and release date and location. The capture tables reported sampling agency and project, sampling gear, capture date and location, habitat type, recapture designation (Y/N), PIT tag number, and fish length, weight, sex, reproductive condition, and status (live or dead).

Recognizing that data in both hatchery and field sampling tables originated from many sources and that human, as well as technological, errors occurred, I conducted thorough error-checking and standardization of database records prior to inclusion in a final data set for analyses. A series of queries was used to detect errors within and among records including missing PIT tag numbers; PIT tag numbers with omitted or extra digits, incorrect characters, or scientific notation format; duplicate records; incorrect recapture designations; and incomplete location data. Tag numbers with missing and extra digits were detected with a simple query to return fields less than or greater than a specific length. Another query searched for records with any characters other than 0 through 9 and A through F, the current range of alpha-numeric characters used in PIT tag codes. Since batches of PIT tags are distributed in series, with each tag varying from others often by only one alpha-numeric character, corrections to PIT tag numbers were rarely made. Such tag numbers were excluded from analyses. PIT tag numbers in scientific format likely originated from formatting of initial data entry files for tags containing the letter "E" and could not be changed in Access. Duplicate records were removed. Recapture designation corrections required the most attention. Individual PIT tag numbers linked hatchery release data to capture data collected during field sampling. Whenever a stocked razorback sucker's tag was encountered in capture data, its recapture designation should have been "Y" (recaptured) and was corrected when necessary. Similarly, captured fish with recapture designations of "Y" should have hatchery release data in most cases. However, it is possible that the first capture record of a tagged razorback sucker was for a wild or untagged hatchery fish, where the fish was implanted with a new tag upon capture and recapture designation of "N" was recorded. That tag number would not link back to hatchery release data and would not be included in further analyses. Since most stocking events occurred at relatively few locations within a river each year, missing stocking locations (river miles) in hatchery release data were easily obtained by consulting hatchery personnel.

Group and covariate identification.—Database fields for inclusion in analysis were selected based on factors that may affect hatchery-reared razorback sucker survival and/or capture probability, including: fish TL, fish weight, river reach, hatchery of origin, year, season, and sampling effort. Data could act as individual, environmental, continuous, or categorical covariates.

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 stocked batch and all other stocking information (year class, lot number, date) was identical among records for that batch, I calculated the mean of reported lengths and assigned it to remaining records for that batch of fish. Records without fish lengths at stocking were excluded from analysis. The potential importance of fish TL as a covariate in analysis was determined an acceptable tradeoff for the exclusion of the relatively few records without length information.

Some covariates were obtained by converting available data to desired formats: river kilometers of release locations were assigned to river reaches and stocking dates were converted to stocking seasons. Based on previous studies (Osmundson and Burnham 1998, Osmundson et al. 1998, Bestgen et al. 2007a) and information about river gradient and geomorphology, I divided the UCRB into seven river reaches (Figure 5). Of those, five reaches had received stocked fish on at least one occasion during the study period: CO2 (Colorado River from upstream of Westwater Canyon to Price-Stubb diversion, RK 200.1 – 303.2; plus Gunnison River downstream of Redlands diversion, RK 0.0 – 4.9), CO3 (Colorado River from Price-Stubb diversion upstream to Rifle, RK 303.3 – 390.0), GU2 (Gunnison River upstream of Redlands diversion, >RK 4.9), GR1 (Green River from Colorado River to just downstream of Desolation-Gray Canyon, RK 0.0 – 206.0), and GR3 (Green River from upstream end of Desolation-Gray Canyon to mouth of Whirlpool Canyon, RK 347.8 – 540.0). Anticipating that comparisons of survival rates among stocking locations would be of interest, I treated the five reaches as groups into which all stocking records would be arranged. An alternative would have been to include "river reach" as an individual covariate, which would have allowed similar comparisons, but increased estimation time.

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

Annual sampling effort within each reach was defined at three levels (Table 1): A (any sampling less intense than either multi-pass Colorado pikeminnow abundance estimate sampling [CS] or multi-pass non-native fish removal sampling [NNF]), B (CS or NNF, plus any lesser sampling), and C (sampling targeting razorback suckers and/or CS plus NNF). Sampling locations, dates, frequencies, and gear for all studies were considered when assigning effort levels.

Redundant and surrogate covariates were eliminated to reduce confounding. For example, measures of fish length and weight provide redundant information (Beckman 1948, McAda and Wydoski 1980, Dowling et al. 1996, Didenko et al. 2004), and the effects of each could not be separated if both were included in analysis. Therefore, weight was eliminated as a covariate. Hatcheries that stocked fish during the study period included Ouray National Fish Hatchery (USFWS, Vernal, Utah), Wahweap Warmwater Hatchery (UDWR, Big Water, Utah), and 24-Road Fish Hatchery (USFWS, Grand Junction, Colorado). Hatcheries were generally assigned to stock a particular river or reach, such that all reaches, except GR1, were stocked by a single source hatchery. Reach GR1 was stocked with razorback suckers from both the 24-Road Fish Hatchery (n = 8,177 from 2003 to 2005) and Ouray National Fish Hatchery (n = 4,388 in 2004). Therefore, river reach may act as a surrogate covariate for hatchery. Stocking year could supply information relating to any annual variation (environmental conditions, hatchery circumstances, or sampling variation). Rather than include year as an individual covariate and, thereby, increase computation time, the effect could be modeled by simply allowing the parameters to vary by time (see "time variation" in "*A priori model set development,*" below). Stocking season is another covariate which provides information about environmental conditions that may vary at frequencies greater than annually, such as discharge, water temperature, and habitat availability at time of stocking. Such environmental data is not in the database and would not only be time-consuming to obtain, but may be confounded with season if added as covariates. Thus, I determined that stocking season as defined was a suitable surrogate for other seasonally varying, but potentially confounded, covariates.

Records were summarized to determine the numbers of razorback suckers stocked across years, seasons, and river reaches and, thereby, assess the balance of data. Any groups, covariates, or combinations lacking data were identified in order to determine inestimable parameters.

Encounter history creation.—An encounter history is a series of 1's (individual captured in the occasion of interest) and 0's (individual not captured) that describes the capture history of an individual animal over the duration of the study; it is the basic data input format for computations. I constructed razorback sucker encounter histories by building an Access query that returned stocking year and subsequent capture years for every stocked fish in the hatchery release table. Capture occasions occur annually and the time interval between capture occasions for this study was defined as one 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 stocking regimes and sampling efforts 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 <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 (e.g., 2003 and 2004) were considered two occasions, even though they may have been at large <12 months (e.g., stocked in September 2003, recaptured in May 2004).

In addition to the encounter history, an input data line must include the encounter history's frequency in the group (stocking reach) to which it belongs, followed by all individual covariate values. The frequency of an individual encounter history is always "1" by definition, except when a fish has died upon recapture, when its frequency would be "−1." To reduce the size of input files, frequencies of duplicate encounter histories were pooled. The data lines were saved as a text file.

Statistical modeling.—Data was analyzed in Program MARK (White and Burnham 1999) using the Cormack-Jolly-Seber (CJS) open population model (Cormack 1964, Jolly 1965, Seber 1965), which assumes: 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 read correctly, 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 capture probability for each time interval, and parameter estimates are conditional on the model used (Burnham et al. 1987).

Parameters of interest in CJS models for this study are apparent survival and capture probability. Apparent survival, φ_j, is the conditional probability of survival in interval *j*, given 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. Capture probability, p_j, is the conditional probability of capture or 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. The random variable, m_{ij}, is the number of recaptures in year *j* from releases in year *i*.

A priori model set development.—After preparing the final dataset for input, I used the previously identified groups and covariates to build an a priori model set. Additional effects were modeled directly within MARK. For each parameter, effects would be modeled individually, additively, or as interactions. Survival rate, φ, model structures included the following effects:

group (*g*) - survival rate estimates vary by river reach into which fish were stocked (CO2, CO3, GU2, GR1, GR3);

constant (.) - no variation; constant survival rate for all individuals and intervals across the study period;

time variation (*t*) - each survival interval has a unique survival rate estimate;

1st river year (ry1) - 1st-interval survival rates 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 stocking than if it is a subsequent interval);

season (season) - 1st-interval survival rate estimates vary by season during which fish were stocked (winter, spring, summer, autumn);

total length at stocking (TL) - 1st-interval survival rates are (linearly) related to total length at time of stocking; a squared term (TL^2) was added to model the more plausible quadratic relationship of survival increasing with increasing total length, up to a maximum point, then decreasing; a cubic term (TL^3) was added to prevent the survival curve from decreasing for the longest total lengths, because that is not a reasonable expectation.

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

group (*g*) - capture probabilities vary by river reach into which fish were stocked (CO2, CO3, GU2, GR1, GR3);

constant (.) - no variation; constant capture probability for all individuals and occasions across the study period;

time variation (*t*) - each capture occasion has a unique capture probability;

1st river year (ry1) - 1st-occasion capture probabilities are different from subsequent-occasion probabilities (i.e., for a given capture occasion (year), fish have a different capture probability if it is their first capture occasion in the river after stocking than if it is a subsequent occasion);

total length at stocking (TL) - 1st-occasion capture probabilities are (linearly) related to total length at time of stocking; a squared term (TL^2) was added to model the more plausible quadratic relationship of capture probability increasing with increasing total length, up to a maximum point, then decreasing; a cubic term (TL^3) was added to prevent the curve from decreasing for the longest total lengths, because that is not a reasonable expectation;

effort (eff) - capture probability of fish stocked into a river reach varies by the sampling effort expended in that reach in subsequent years.

Run procedure and model selection.—Because the large dataset and numerous a priori model structures for each of the φ and *p* parameters required extensive analysis, a more efficient procedure to run candidate models was employed. A global model, which contained many of the influential effects and fit the dataset reasonably well, was chosen. For initial runs, the complex structure for the φ portion of the global model remained the same, while the *p* portion was kept simple. 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 global φ structure, the p structure from the best model (see below) was retained and run with all variations of φ, starting with the simplest structure. I ran all models using the logit link to maintain a monotonic relationship with the continuous individual covariate, TL.

Model selection was conducted using 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.

Movement

Whereas time intervals were defined as one year and multiple within-year captures were counted only once for φ and p parameter estimation, all capture information (with the exception of multiple same-day recaptures) was used to describe movement of stocked razorback suckers. Therefore, razorback suckers stocked and recaptured in 2006 were added to the dataset. For each tagged fish with any recapture event, I compiled the following data for both stocking and recapture occasions: river, reach, RK, and date. Distance between locations 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

Parameter estimation

Dataset summary.—The final dataset 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* = 68,916) in autumn (Table 2), followed by summer, spring, and winter, in descending order. Stocking did not occur every year in all reaches (Table 3). Overall, most fish were stocked into the Colorado River (*n* = 61,282) and in reach CO2, in particular (*n* = 44,542). Fish lengths at stocking ranged from 75 – 586 mm TL (Figure 6) with a mean of 252.5 mm TL. Mean lengths of stocked fish per season ranged from 224 mm TL in spring to 280 mm TL in summer (Table 2). 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 3).

Captures of stocked razorback suckers occurred on every capture occasion from 1997 through 2006, but not in 1996. Years 2005 and 2006 produced the most captures (*n* = 463 and *n* = 428, respectively), as did the Colorado River, in general, and reach CO2 (*n* = 441), specifically (Table 4).

The largest portions of recaptures consist of fish stocked in 2004 (*n* = 412) or those stocked into reach CO2 (*n* = 601, Table 5). 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), and winter (*n* = 112). Lengths at stocking for razorback suckers that were subsequently recaptured ranged from 129 – 495 mm TL with mean of 327 mm TL (Figure 7).

A priori model set.—Appendix A.

Model selection.—Analysis resulted in a much more reduced set of reasonable models than was expected. This was because relatively parameter rich models that included interactions of group and time effects produced so many inestimable parameters that they were removed from consideration. There were more than 50 models in the resulting model set (Appendix B), 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 6), and the second-best model was about 10 AIC_c points away. 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.

Parameter estimates.—The top-ranked model contained 24 estimable parameters. Survival was modeled with 7 parameters: an intercept, 1st-interval effect, 3 stocking season effects, and both linear and quadratic effects of TL. The intercept represented the fourth season. Parameter values for the function of logit φ were: 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). Since autumn was represented by the intercept, its parameter value (difference from intercept) was 0.0000. Large negative logit values for effects ry1 and summer indicate lower survival in those times. The model resulted in 5 survival rate estimates, including four 1st-interval, TL-dependent φ's 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 1st-interval survival rates, ry1 φ's, of razorback suckers stocked in the Upper Colorado River Basin (Figure 8). 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 >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, 1st-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% confidence limits for 1st-interval and subsequent-interval estimates do not overlap until total length at stocking reaches 415 mm.

Season of stocking also had a large effect on 1st-interval survival of razorback suckers. Survival patterns over a range of lengths at stocking were similar for fish stocked in autumn, winter, and spring (Figure 9). However, survival was comparatively much lower for fish of all sizes when stocked in summer. For example, 1st-interval survival rate for razorback suckers of average length (252.5 mm TL) stocked in summer was <0.02 (95% CI: 0.012 – 0.022), but was 0.08 (0.057 – 0.100), 0.08 (0.057 – 0.118) and 0.07 (0.044 – 0.094) for fish of the same length stocked in autumn, winter, and spring, respectively. The same pattern was observed for fish stocked at the currently recommended length of 300 mm TL (Nesler et al. 2003) and even 400 mm TL (Figure 10), which suggested a large effect of season on survival, regardless of fish size. Survival rate estimate confidence limits for razorback suckers stocked in summer do not begin to overlap with those of any other season until length at stocking reaches 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 is independent of fish length at stocking and stocking season.

In the 24-parameter top model, capture probability was modeled with 17 parameters: an intercept, 4 group parameters, 10 occasions (one was inestimable), 1st-occasion effect, and both linear and quadratic effects of TL. The intercept represented the fifth group on the eleventh occasion. Parameter estimates for the function of logit *p* (Table 7) produced 105 capture probability estimates, including 11 time-varying, 1st-occasion, TL-dependent *p*'s and 10 time-varying, subsequent-occasion *p*'s for each of the 5 river reaches where fish were stocked. However, since no fish stocked in 1995 were recaptured, the 1996 capture probability was inestimable for all 5 groups, which reduced the number of estimates of *p* to 100.

Capture probability estimates were all relatively low, ranging from 0.002 – 0.128 for razorback suckers of average length at stocking (Table 8). Razorback suckers stocked into reach GR1 produced the highest *p*'s, followed by CO2, GR3, CO3, and GU2, in descending order. Although 1st-occasion (ry1) capture probability estimates were higher than subsequent-occasion (post-ry1) estimates, the two estimates did not differ for any capture occasion within any group, based on overlapping 95% CIs. However, capture probabilities (ry1 or post-ry1) differed significantly 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 (TL) at stocking (0.0.106, 95% CI: −0.0023 – 0.0237) did not differ significantly from the intercept, suggesting that TL had little effect on capture probabilities.

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, 2,748 contained information on both distance traveled and time elapsed since stocking or previous recapture. Distance, timing, and rates of razorback sucker movements varied widely over the study period (Table 9). Mean distance traveled by a razorback sucker on any leg was 54.7 RK (range: 0 – 514.9). The maximum distance traveled was produced by a fish moving from reach GR3 to CO1 over 410 days (rate = 1.25 RK/d). The 294 mm TL razorback sucker was stocked in the Green River at RK 514.1 (downstream of Split Mountain) in April 2003 and recaptured (the only time during this study period) in the Colorado River at RK 0.8 in May 2004 when it measured 390 mm TL. The distance is remarkable, given that only about 15% of legs traveled exceeded 100 RK and only 1.5% exceeded 300 RK. Mean time elapsed from one recapture event (or stocking) to next recapture event was 254 days (range: 0 – 3,164). The maximum time elapsed (3,164 days = 8.8 years) was from a 362 mm TL razorback sucker stocked during October 1996 in the Gunnison River (RK 91.8) and recaptured in June 2005 in the Colorado River (RK 213.0), a difference of 153 RK. It measured 490 mm TL upon recapture. The mean rate of movement for all legs traveled by all razorback suckers was 0.87 RK/d (range: 0 – 55.37). Mean distance traveled, time elapsed, and rate of travel per fish (from stocking to last recapture) were 60.0 RK, 278 days, and 0.91 RK/d, respectively. Distance, time, and rate were all highest for initial legs (stocking to first capture event) than subsequent legs (Table 9).

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 not actually movements at all: they were recaptures of razorback suckers at the same locations as their previous captures, resulting in no direction of movement.

Within any one of the three mainstem rivers (CO, GU, GR), mean downstream distance moved was 52.9 RK, while mean upstream distance moved was 22.9 RK. Travel among all three rivers within a leg produced the longest mean distance traveled, 454.6 RK. Travel in a leg involving a tributary produced a mean distance of 186.3 RK 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 and Gunnison River subbasins than in the Green River subbasin (Table 10). While only 7.7% (range: 2.9 – 10.3%) of fish stocked into Green River reaches were ever recaptured outside of their original stocking reaches, 36.9% (range: 30.1 – 100%) of those stocked into the Colorado or Gunnison rivers were eventually recaptured outside of their stocking reaches.

Movement frequencies out of reaches CO3 and GU2, in particular, were very high. All razorback suckers stocked into reach CO3 were recaptured in downstream reaches CO2 or CO1, and nearly half of those stocked into reach GU2 were recaptured 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. Fish stocked into reach CO2 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 remained there, moved down to CO2 or CO1, or moved down then upstream into GR1. Fish stocked into GR3 remained in the reach (including Duchesne and White rivers), moved downstream into reaches GR2 or GR1 (including 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. Movement frequencies between reaches, regardless of stocking locations, were similar (Table 11).

Razorback suckers stocked during winter moved the longest distances on average (86.7 RK), but those stocked in summer moved at the highest rates on average (1.34 RK/d, Table 12). There was no discernible pattern in mean distances traveled by fish stocked at sizes greater than 150 mm TL, but fish smaller than that moved less than 20 RK over 13 or fewer days on average (Figure 11).

Discussion

Parameter estimation

1st-interval and subsequent-interval survival.—Survival rates of stocked razorback suckers through their first intervals in the river were significantly lower than those through subsequent intervals for fish of nearly all lengths at stocking. While the integrated stocking plan for razorback suckers anticipated variable survival rates (Nesler at al. 2003), the assumptions related solely to age and size of stocked fish rather than time since stocking. This result is not particularly surprising, given the relatively benign hatchery environment in which fish are raised for 2 – 3 growing seasons prior to stocking. That environment includes stable or no flow velocity, constant temperatures, dependable and abundant food, and predator-free habitats, which 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. For example, white sturgeon (*Acipenser transmontanus* Richardson) stocked into the Kootenai River, Idaho, exhibit first-year survival rates 30% lower than in subsequent years (Ireland et al. 2002). Hatchery-reared bonytail, a Colorado River Basin endangered species, 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. In press). Razorback suckers have demonstrated poor post-stocking survival in several studies. Marsh and Brooks (1989) estimated that 900 razorback suckers/km could be consumed by ictalurids within 24 h of being stocked in the Gila River, Arizona. Marsh et al. (2005) estimated first-year survivorship to be ≤ 0.26 for most razorback suckers stocked in Lake Mohave from 1999 – 2002.

The survival rate result for stocked fish in post-ry1 intervals is more encouraging: hatchery individuals survive at rates similar to their wild counterparts after their first year in the river. The estimated survival rate for any stocked razorback sucker through any interval subsequent to its first interval in the river was 0.75, a rate similar to 0.70 assumed in the integrated stocking plan for age-4 (adult) fish (Nesler et al. 2003). It also agrees with the 0.71 (SE = 0.0246) survival rate estimated for wild adult razorbacks in the middle Green River from 1980 – 1992 by Modde et al. (1996). Bestgen et al. (2002) built on that dataset and estimated survival of wild razorbacks in the Green River basin to be 0.73 (SE = 0.0287) from 1980 – 1992 and 0.76 (SE = 0.0475) from 1990 – 1999. Fish captured in the 1980 – 1992 dataset were primarily marked with dorsally-attached Carlin tags, which have a greater propensity for loss than PIT tags employed in the later dataset and in this study (Prentice et al. 1990, McAllister et al. 1992, Ombredane et al.

1998, Ward and David 2006). Even though actual tag loss is assumed to be low for this study, faulty scanning equipment, lack of scanning, and data recording errors all result in virtual tag loss and biased estimates of survival (Bestgen et al. 2002). Of the 4,010 total razorback sucker capture events in the database, at least 275 records (6.9%) had PIT tag errors which made them unusable in analyses. Because recapture rates are already relatively low, careful tag detection becomes even more vital to effective parameter estimation. Nevertheless, high post-ry1 survival rates and observations of stocked razorback suckers in spawning aggregations with wild individuals (Modde et al. 2005) suggest that hatchery-reared fish are capable of acclimating to the wild environment.

While many hatchery operations simply target specific numbers and sizes of fish, investigations have begun to address underlying causes of post-stocking mortality. Aside from stress related to handling and transport, post-stocking predation and lack of conditioning have been suggested as explanations (Marsh and Brooks 1989, Mueller et al. 2003). Exposure to chemical cues of a predator (pike odor and trout skin extract with alarm signal) successfully induced anti-predator behavior in rainbow trout (Brown and Smith 1998). Olla et al. (1998) demonstrated that training fish to exhibit anti-predator behavior through social learning from conspecifics reduced susceptibility. Exercise conditioning was found to increase swim performances of razorback sucker by 26% (Ward and Hilwig 2004). Combined predator exposure and exercise conditioning showed promising results for razorback sucker survival: treatment fish (exercised and exposed to predation) experienced significantly lower mortality in the presence of flathead catfish (*Pylodictis olivaris* Rafinesque) than unexercised, predator-naïve fish (31% ± 4.41 SE and 46% ± 4.88 SE, respectively; 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 significantly higher mortality rate for control fish was conservative compared to a truly naïve group, unable to learn from more predator-savvy conspecifics. Ultimately, predator-avoidance training and conditioning of hatchery-reared razorback suckers may increase low 1st-interval survival.

Moreover, hatcheries rearing razorback suckers have begun moving some fish from indoor tanks to outdoor grow-out ponds to provide an environment more similar to natural conditions (T. Czapla, U. S. Fish and Wildlife Service, personal communication). Analysis of post-release recapture information for pond-reared vs. tank-reared fish may be useful to evaluate if pond-rearing enhances 1st-year survival rates. However, relevant data on rearing history must be accurately and consistently recorded for each individual fish for such an analysis to proceed.

Stocking length and 1st-interval survival.—In addition to predator naïveté and hatchery conditions that likely affect 1st-interval survival of all stocked razorback suckers, total length at time of stocking is also a strong influence. Larger fish survive their first intervals in the river better than smaller ones, which underscores the need to continue to collect length information on hatchery-reared razorback suckers prior to stocking. While TL undoubtedly affects razorback sucker survival in subsequent intervals, I did not model that effect in this study. Total length at capture was not recorded for every recaptured fish, and with so few recapture records available, I did not want to leave any out of analysis. I did, however, allow total length *at stocking* to influence all survival intervals (Appendix B), but those models fell well below the top model.

Hypothesized survival rates in the razorback sucker integrated stocking plan are overestimated for all ages (and, therefore, total lengths) at stocking. Fish stocked at age-2 (approximately 300 mm TL) were assumed to survive at a rate of 0.50, while my analysis predicted survival of 2 – 10 times less, at 0.05 – 0.21, depending on stocking season. Similarly, it was assumed that razorback suckers stocked at age-3 (300 – 399 mm TL) would have a 0.60 survival rate, but the model predicted 0.12 – 0.42 for a 350 mm TL stocked fish. Even adult fish (≥ age-4 and 400 mm TL) do not survive at the assumed 0.70 rate during their first interval, but rather 0.23 – 0.62. First-year survival rates later estimated for repatriated razorback suckers in Lake Mohave followed a trajectory similar to, but steeper than, those in this study, with 300 and 350 mm TL stocked fish surviving at rates of 0.10 and 0.26, respectively (Marsh et al. 2005). The effect of TL on 1st-interval survival may, again, relate back to predator avoidance (i.e., evasion or exceeding predator gape limit) and conditioning (i.e., ability to withstand current and seek suitable habitat). Evidence to support that hypothesis is from Marsh and Brooks (1989), who found a positive correlation ($r^2 = 0.76$, $P < 0.10$) between predator size and lengths of ingested razorback suckers.

Just as sport fish managers have had to weigh the costs and benefits of raising many, smaller fish or fewer, larger fish in their hatcheries (Heidinger 1993), so must managers charged with the recovery of razorback suckers. Growing larger fish would increase 1st-interval survival, but requires more space, food, and time; however, not doing so equates to wasting most of those resources expended to raise fish to sizes inadequate for meeting razorback sucker recovery goals. A cost: benefit analysis is necessary to quantify the trade-offs and determine the most effective path to achieving those goals.

Stocking season and 1st-interval survival.—Stocking season greatly affected 1st-interval survival of razorback suckers. Those stocked in summer (June, July, or August) survived at significantly lower rates than those stocked during any other season. A concern with analyzing survival by season of stocking was that razorback suckers stocked earlier in a year may have been susceptible to 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 for fish stocked in spring, followed by summer, autumn, and winter, in ascending order. However, my results showed tight grouping of spring, autumn, and winter 1st-interval survival curves (Figure 9) and confidence limits of the survival rate estimate for summer-stocked razorback suckers that did not overlap those of any other stocking season. Therefore, I concluded the effect of stocking season was not simply a measure of the amount of time fish were susceptible to mortality and that legitimate seasonal differences in survival exist.

Since the model used to calculate seasonal survival rate estimates also included length at stocking, I was suspicious that season and TL might be confounded (i.e., the smallest fish were stocked during summer). On the contrary, the largest razorback suckers, on average, were stocked in summer (mean: 280 mm TL, range: 75 – 586 mm TL, Table 2), and fish released in spring accounted for more than 81% of the smallest fish stocked in the study (<100 mm TL, Figure 12). I concluded, therefore, that the effect of summer stocking was valid and not confounded with total length.

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, often reaching a daily mean >25°C in middle Green River near Jensen, Utah (USGS gage 09261000), 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 captured in the Green River 2 – 4 months later all had fungal infections and/or *Lernea* sp. (Bestgen et al. In press). Furthermore, several predaceous species introduced into the Upper Colorado River Basin, such as centrarchids and ictalurids, are more active in warm water than in cold water. Marsh and Brooks (1989) found that 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. The integrated stocking plan for razorback sucker lists autumn as the primary stocking season and spring/summer as the secondary stocking seasons for culled fish that require more time to attain the required stocking length (Nesler et al. 2003). Stocking events for this study period followed that pattern, with most fish stocked during autumn and then summer, respectively. Considering the extremely low survival rate for razorback suckers stocked in summer, releases during those months ought to be avoided and the stocking plan should be amended accordingly.

Reach, time, and survival.—Neither stocking reach nor stocking year significantly affected survival of stocked razorback suckers during the study period. 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 should be investigated in future survival rate analyses. If stocking protocols become more consistent, as expected under the integrated stocking plan, and only those reaches which retain reasonable numbers of fish are included in analysis, estimation of razorback sucker survival rates per reach should be attainable. Those estimates, in turn, would aid in achieving the minimum population sizes required per subbasin for downlisting the species. It should be noted, however, that subbasin survival rates and associated population size estimates only address a portion of the razorback sucker recovery goals. The maintenance of those population size targets over time must be monitored using trend analyses (e. g., population rates of change) to satisfy recovery criteria.

Stocking year is likely not an insignificant effect on the survival of stocked fish. Low flows associated with recent drought years may reduce available habitat for stocked razorback suckers, resulting in crowding, increased disease transmission, and increased encounters with native and nonnative predators (Bestgen et al. 2007a). However, the imbalance of stocking and recapture data may have 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 per year ranged from <1,000 – >30,000. Furthermore, fish were not stocked into every reach in every year (Table 3), making investigations of interactive effects among reaches and years impossible. In order to better understand effects of stocking reaches and years on survival, future analyses should employ a more balanced dataset generated through continued implementation of the integrated stocking plan.

Apparent survival, φ, vs. true survival, S.—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, $1 - \varphi$ represents the probability that individuals either die or emigrate to areas where they are not susceptible to capture. In this study, apparent survival closely approximates true survival because most fish were susceptible to capture. This is because sampling covered most of the UCRB and very few fish are ever encountered in the canyon-bound reaches of the Colorado River, including upper Lake Powell, downstream of its confluence with the Green River.

Capture probability.—Capture probability, *p*, is referred to as a "nuisance parameter" because it is not the primary parameter of interest. It is, however, inextricably linked to survival estimation:

$$\log_e \mathcal{L}(\varphi, p \mid \text{EH}) = \sum(\text{\# of animals}) * \log_e(\text{Probability[EH]}),$$

which states that the log-likelihood of the parameters, given the encounter histories 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 capture probabilities (or 1 – capture probabilities, if not captured) for all intervals and occasions. Increasing capture probabilities results in more precise survival estimates

(Lebreton et al. 1992), so it is worthwhile to design studies with that in mind. In this case, time since stocking, size of stocked fish, stocking reach, and capture year are factors that can affect capture probability.

1st-occasion and subsequent-occasion capture probability.—For any given capture occasion (sampling year), capture probability was slightly, but not significantly, higher for fish when it was their 1st capture occasion after stocking than if it was a subsequent capture occasion (Table 8). Overall, both probabilities were low: the highest achieved for the average-sized stocked razorback sucker was 0.13. In mark-recapture studies, one aims to capture the most individuals from a released cohort on the first occasion after initial marking (stocking), which equates to high capture probability. One reason that this study did not always accomplish that aim is that data were collected from various sampling efforts, very few of which specifically targeted stocked razorback suckers. Future capture 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.

Stocking length and 1st-occasion capture probability.—The parameter estimate for total length at stocking was not significantly different from the model's intercept, although larger stocked razorback suckers had slightly higher capture probabilities than smaller ones. For example, 1st-interval capture 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 13) when the size of stocked fish increased from the mean length (252.5 mm TL) to 400 mm TL. While that translates to a 25% increase, the effect is minor due to the extremely low capture probabilities estimated overall. More notable is that razorback suckers stocked at larger sizes were captured at rates higher than those at which they were stocked (Figure 14), regardless of capture occasion. For instance, fish stocked from 250 – 299 mm TL accounted for 29.1% of all fish stocked, while only 24.3% of recaptures consisted of fish stocked in that size range. Conversely, fish stocked from 300 – 349 mm TL comprised 20.6% of the total stocked, but that range of lengths at stocking made up 39.1% 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 Upper Colorado River Basin, both higher for fish stocked at greater lengths. 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 better than smaller ones (Dolan and Miranda 2003, Snyder 2003). So it is not surprising that fish stocked at larger sizes were captured at higher rates. Higher capture rates would be an additional benefit of stocking larger razorback suckers and should be considered when weighing the costs and benefits of increasing lengths at stocked fish.

I ran a model without the effect of stocking length on 1st-occasion capture probabilities. This produced a model which was less than 1 AIC_c point from the top model. However, that model was not considered further, because length at stocking had such a pronounced effect on survival of hatchery-reared razorback suckers and effect of length on capture probability is generally an important feature of capture-recapture studies of fishes. Therefore, I retained the 1st-occasion TL effect in the p structure of the model.

Reach, time, and capture probability.—Other factors that affected capture probabilities were stocking reach (group, g) and capture occasion (time, t). The interaction of the two did not produce estimable parameters, likely a result of the data imbalance across stocking reaches and years discussed earlier. The additive effects of the factors, however, did make it into the top model. Overall, razorback suckers stocked into reach GR1 had the highest capture probabilities, followed by those stocked into reaches CO2, GR3, CO3, and GU2, in descending order (Table 8). It must be noted that capture 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 10), but enough were found elsewhere that the distinction becomes important. Suggested solutions to avoid confusion included: 1) adding "capture reach" as an individual covariate, which would allow capture probability to relate to both stocking reach and capture reach and 2) conducting a multistate analysis (e.g., Bestgen et al. 2007), which would estimate the probabilities of fish transitioning from one state (reach) to another. However, some razorback suckers were captured 3 times throughout the study period, each time in a different reach, making the assignment of a single individual covariate impossible for many individuals. The data did not contain enough of those between-reach movements, however, to warrant a multistate analysis. Furthermore, a critical assumption of that analysis is "transitions take place immediately before encounter occasions" (White et al. 2006), which could not be met in this study. Consequently, a multistate analysis may have estimated transition rates, but would not have produced distinguishable survival rate estimates among reaches, which I hypothesized to be of importance in this study. Therefore, I proceeded with capture probabilities referring solely to fish stocked into particular reaches, regardless of where they were recaptured.

There were only a few significant differences among capture 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). I attempted to simplify estimation by categorizing the 11 years of sampling effort in each stocking reach into 3 levels (Table 1), but the model may not have been complex enough to account for the heterogeneity. Furthermore, effort expended in a reach does not always relate directly to capture probabilities of fish stocked into that reach, as many are captured elsewhere. For example, fish stocked into reach CO3 had some of the lowest *p*'s, and one might conclude that limited sampling through the years is responsible. However, all fish stocked into CO3 were, in fact, captured downstream in more heavily sampled reaches CO2 and CO1. Similarly, fish stocked into GU2 had the lowest *p*'s and the reach experienced the least sampling (flow investigations from 2003 – 2005). However, almost half the recaptures of fish stocked into GU2 occurred in reach CO2. Since models including effort effects did not produce clear or constructive results, they were left out of analysis. However, information about annual sampling within the basin remained useful when investigating observed differences among capture probabilities in the time-varying top model.

Sampling heterogeneity, fluctuating stocking numbers, and environmental factors may all contribute to annual variation among *p*'s. Capture probabilities for 1996 were inestimable for razorback suckers stocked in all reaches, because no fish stocked during 1995 were recaptured. Capture probabilities in 1998 were the lowest of all estimable years, despite the fact that sampling in that year occurred in nearly all reaches and included monitoring of razorback sucker in the Green River subbasin and intensive Colorado pikeminnow abundance estimate sampling in the Colorado River subbasin. Stocking of razorback suckers in previous years (1995 – 1997), however, occurred in only one or two reaches (GU2 and GR3, Table 3), was limited to approximately 1,000 – 3,000 fish per year, and could have contributed to the low *p* estimated for 1998. Capture probabilities increased steadily from 1999 through 2001, but declined again in 2002. Sampling that year was notably absent in the Colorado and Gunnison River subbasins, but due to fish movement into reaches where sampling did occur, sampling effort in a stocking reach does not directly correspond to capture probabilities. Numbers of stocked razorback suckers varied in the years prior to 2002, but had increased overall since stocking began, with more than 30,000 fish released in 2000. This suggests that increasing numbers of stocked fish does not necessarily result in increased capture probabilities in ensuing years. Another explanation for low 2002 capture probabilities is environmental: it was one of the worst drought years on record for the Upper Colorado River Basin. For example, mean flow of the Green River at Jensen, Utah, was the second-lowest reported since 1947 (U.S. Geological Survey gage 09261000, Figure 15). Low flows may have impeded boat and raft sampling and certainly reduced the length of the usual sampling season. Associated high water temperatures may have caused fish to remain more sedentary and/or occupy deeper, pool habitats, making them less susceptible to capture. As stated previously, future studies should employ uniform stocking procedures and consistent, targeted effort in order to better understand how the above factors affect capture probabilities of razorback suckers.

Movement

Distance, time, and rate.—The initial legs of all razorback sucker movements resulted in the longest distances traveled per leg, most time elapsed between legs, and highest rates of travel per leg, implying that most movement occurs between stocking and first recapture event. This was likely due to razorback suckers exploring their new environment and seeking suitable habitat. Those three measures of movement declined by 28 – 95% on subsequent legs, perhaps after most fish found preferred habitats.

Direction.—Most movements, regardless of leg, were in a downstream direction. It is unknown if downstream movements are active, intentional movements to reach 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).

Reach.—There were not enough movements among reaches to warrant a multistate analysis, which would have estimated the probabilities of razorback suckers transitioning from one reach to another. Some movement differences among reaches, nevertheless, are 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 experience the highest percentages of departures happen to be the shortest stocking reaches in the study area: reaches CO2, CO3, and GU2 are about 103, 87, and 92 RK in length, respectively, while GR1 and GR3 are 192 and 206 RK 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 are longest, on average, for razorback suckers stocked into the two shortest reaches (Table 13), nearly twice as long as those for fish stocked into other reaches. The two shortest reaches also produced the 1st and 3rd highest rates of initial-leg movements, which suggested that movement out of reaches CO3 and GU2 were not more frequent due to reach length alone. Since there were few or no significant differences in survival and capture 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 placing large numbers of hatchery-reared razorback suckers into stocking reaches from which a large percentage of fish leave should be assessed.

Stocking season.—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, likely 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.

Summary

Hatchery-reared razorback suckers survive their first year in the river at rates considerably lower than the rates assumed in the species' stocking plan. After their first year, however, fish survive at rates assumed in the species' stocking plan and are similar to those calculated for wild razorback suckers. Initial post-stocking survival was shown to be dependent on total length at stocking and season of stocking: survival rate estimates increased as length at stocking increased, but razorback suckers of nearly all lengths survived at significantly lower rates when stocked during summer compared to any other season. Capture probabilities were low overall, with only minor differences among reaches and years. Fish stocked at larger sizes were captured at rates higher than those at which they were stocked, but increasing total length at stocking only minimally raised the already low capture probabilities.

The integrated stocking plan assumes variable, age-related survival rates of hatchery-reared razorback suckers and defines the stocking protocol intended to reestablish self-sustaining populations in the UCRB, the foundation of the species' recovery goals. As the plan evolved, more consistent stocking practices across time and space were employed, which made this survival rate estimation possible. Based on these results, however, assumed survival rates are not realized by stocked razorback suckers and the protocols should be reevaluated. In particular, stocking during summer months should be halted and a cost:benefit analysis of total length at stocking and associated survival should be conducted. Suggested reasons for low 1st-interval survival of razorback suckers (predation, lack of conditioning) should be investigated further. Additionally, estimation of effects of specific rearing or stocking procedures (such as rearing solely in tanks vs. both tanks and grow-out ponds) could use a reduced, more balanced dataset focused on years in which the technique was employed. Changes to the stocking plan should be monitored with continued survival rate estimation, using data collected from uniform sampling efforts designed to maximize capture of razorback suckers. Finally, measurement of progress toward razorback sucker recovery may be improved using population trend analyses within each subbasin and for the entire Upper Colorado River Basin as a whole, in addition to minimum subbasin population size targets already defined in the species' recovery goals.

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. This study provides managers with accurate survival estimates for stocked fish and factors that influenced those estimates, essential tools used to evaluate hatchery production strategies and stocking protocols. These results will immediately advance recovery prospects for razorback sucker in the Upper Colorado River Basin.

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Table 1. Annual sampling effort in razorback sucker stocking reaches in the Upper Colorado River Basin, Utah and Colorado, 1996–2006. CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; CO3 = Colorado River, RK 303.3 – 390.0; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0; GR3 = Green River, RK 347.8 – 540.0. Most effort data originated from the Upper Colorado River Basin database, maintained by U. S. Fish and Wildlife Service, Grand Junction, Colorado. This table is not comprehensive, but representative of the degree of sampling that occurred annually per reach.

reach	study[a]	year										
		1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
CO2	ISMP	X	X	X	X	X						
	RZ ST						X					
	HB			X	X	X			X	X	X	
	CS			X	X	X			X	X	X	
	NNF				X	X	X			X	X	X
	FLOW				X	X	X		X	X		
CO3	FLOW	X										
	RZ ST					X	X					
	NNF									X	X	X
	PASS											
GU2	RZ ST	X	X	X	X	X	X					
	PASS	X	X	X	X	X	X	X	X	X	X	X
	FLOW								X	X	X	
GR1	ISMP	X	X	X	X	X						
	BT	X	X	X	X	X	X					
	FM/BH						X	X	X			
	CS						X	X	X			X
GR3	LEVEE	X	X	X	X							
	ISMP	X	X	X	X	X						
	RZ BW	X	X	X	X							
	RZ SP				X	X						X
	CS					X	X	X	X			X
	NNF						X	X	X	X	X	X
	FLP								X	X		

[a] ISMP = Interagency Standardized Monitoring Program (McAda 2002b); RZ ST = stocked razorback sucker monitoring (Burdick 2003); HB = humpback chub sampling (McAda 2002a); CS = Colorado pikeminnow abundance estimation sampling (Osmundson 2002, Bestgen et al. 2007a); NNF = non-native fish removal: northern pike, smallmouth bass, and centrarchids (Osmundson 2003, Bestgen et al. 2007c, Burdick 2008); FLOW = flow and fish investigations (Anderson and Stewart 2007); PASS = fish passage evaluation (Burdick 2001); BT = bonytail sampling (Badame and Hudson 2003); FM/BH = flannelmouth and bluehead sucker sampling (Badame et al. 2004); LEVEE = levee removal (Birchell et al. 2002); RZ BW = basin-wide monitoring of razorback suckers (Bestgen et al. 2002); RZ SP = razorback sucker spawning bar sampling (Modde et al. 2005, Hedrick and Monroe 2006); FLP = floodplain reset experiments (Modde and Haines 2005).

Table 2. Number and total lengths (TL) of razorback suckers stocked per year and season in the Upper Colorado River Basin, Utah and Colorado, 1995–2005. Winter = November and December; spring = March, April, and May; summer = June, July, and August; autumn = September and October.

season	length at stocking (mmTL)		year of stocking											season total
	mean	range	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
winter	229	(78–520)					453	5234		1188		1907	1606	10388
spring	224	(75–497)						4509	60	277	7888	1259	255	14248
summer	280	(75–586)				233	2471	3726	595	2331	3214	3911	9096	25577
autumn	252	(84–530)	1221	1122	2926	760	4588	16581	5544	7852	5262	14652	8408	68916
year total			1221	1122	2926	993	7512	30050	6199	11648	16364	21729	19365	119129

Table 3. Number and total lengths (TL) of razorback suckers stocked per year in five reaches of the Upper Colorado River Basin, Utah and Colorado, 1995–2005. CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; CO3 = Colorado River, RK 303.3 – 390.0; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0; GR3 = Green River, RK 347.8 – 540.0.

river reach	length at stocking (mmTL)		year of stocking											reach total
	mean	range	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
CO2	263	(80–530)						11434	698	10468	5505	6153	10284	44542
CO3	163	(77–388)					3411	11810	1456	52	11			16740
GU2	217	(75–586)	316	287	2926	606	2744	6582	4045	854	25			18385
GR1	296	(171–464)									2377	5957	4231	12565
GR3	294	(127–560)	905	835		387	1357	224		274	8446	9619	4850	26897
year total			1221	1122	2926	993	7512	30050	6199	11648	16364	21729	19365	119129

Table 4. Number of razorback suckers recaptured per year and river reach in the Upper Colorado River Basin, Utah and Colorado, 1996–2006. CO1 = Colorado River, RK 0.0 – 200.0; CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; CO3 = Colorado River, RK 303.3 – 390.0; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0; GR2 = Green River, RK 206.1 – 347.7; GR3 = Green River, RK 347.8 – 540.0.

river reach	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	1388

Table 5. Recaptures of razorback suckers stocked in each reach and year in the Upper Colorado River Basin, Utah and Colorado, 1996–2005. CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; CO3 = Colorado River, RK 303.3 – 390.0; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0; GR3 = Green River, RK 347.8 – 540.0.

stocking reach	stocking year										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	1388

Table 6. Cormack-Jolly-Seber open population models to estimate apparent survival (φ) and capture probability (*p*) for hatchery-reared razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, from 1995 to 2005. The top eight models selected by AIC_C values are shown for comparison. Effects included stocking season (season), group or stocking reach (*g*), time (*t*), 1st interval or occasion in the river (ry1), and total length at stocking (TL and TL^2).

Model	AIC_c	Delta AIC_c	AIC_c Weights	Model Likelihood	Number of Parameters	Deviance
$\{\varphi(\text{ry1+season+TL+TL}^2)\ p\,(g+[\text{ry1+TL+TL}^2+t])\}$	15614.582	0	0.994	1.000	24	15566.582
$\{\varphi(\text{ry1+season+TL+TL}^2)\ p\,(g+t)\}$	15624.877	10.295	0.006	0.006	21	15582.877
$\{\varphi(\text{ry1+TL+TL}^2)\ p\,(g+[\text{ry1+TL+TL}^2+t])\}$	15839.803	225.221	0	0	21	15797.803
$\{\varphi(g+[\text{ry1+TL+TL}^2])\ p\,(g+[\text{ry1+TL+TL}^2+t])\}$	15843.270	228.688	0	0	25	15793.270
$\{\varphi(\text{ry1+TL+TL}^2)\ p\,(g+[\text{ry1}+t])\}$	15844.069	229.487	0	0	19	15806.069
$\{\varphi(g+[\text{ry1+TL+TL}^2])\ p\,(g+[\text{ry1}+t])\}$	15845.244	230.662	0	0	23	15799.244
$\{\varphi(g+[\text{ry1+TL+TL}^2])\ p\,(g+t)\}$	15850.340	235.758	0	0	22	15806.340
$\{\varphi(\text{ry1+TL+TL}^2)\ p\,(g+t)\}$	15854.285	239.703	0	0	18	15818.285

Table 7. Parameter estimates for the function of logit *p*, capture probability, for hatchery-reared razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, from 1995 to 2005. CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; CO3 = Colorado River, RK 303.3 – 390.0; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0; GR3 = Green River, RK 347.8 – 540.0. 1996 through 2005 = capture occasions; ry1 = effect of 1st occasion in the river (vs. subsequent occasions); TL and TL^2 = total length at stocking individual covariates. The intercept represents group GR3 in capture year 2006.

Parameter	Estimate	SE
intercept	−3.3572564	0.163995
CO2	0.215187	0.078327
CO3	−0.3722413	0.248734
GU2	−0.4980765	0.136897
GR1	0.385772	0.098734
1996	−8.7748694	261.046150
1997	−0.2212017	0.471288
1998	−2.4219219	1.010314
1999	0.459633	0.207578
2000	0.555273	0.193812
2001	0.887339	0.155238
2002	−0.6035752	0.229609
2003	0.352959	0.107383
2004	−0.1503319	0.101872
2005	0.325758	0.073123
ry1	−1.6511343	1.148335
TL	0.010690	0.006627
TL^2	−0.0000138	0.000010

Table 8. Probabilities of capture (1st–occasion, ry1 *p*, and subsequent-occasion, post-ry1 *p*, 1996 – 2006) and 95% confidence intervals (CI) for a razorback sucker of average total length (252.5 mm TL) stocked in five reaches of the Upper Colorado River Basin, Utah and Colorado, 1996–2006. CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; CO3 = Colorado River, RK 303.3 – 390.0; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0; GR3 = Green River, RK 347.8 – 540.0.

stocking reach	capture year	ry1 *p*	95% CI		post-ry1 *p*	95% CI	
CO2	1996	0.000	0.0000	1.0000			
	1997	0.039	0.0153	0.0972	0.033	0.0131	0.0831
	1998	0.005	0.0006	0.0325	0.004	0.0005	0.0275
	1999	0.075	0.0461	0.1189	0.064	0.0406	0.0996
	2000	0.082	0.0521	0.1255	0.070	0.0452	0.1069
	2001	0.110	0.0776	0.1542	0.095	0.0658	0.1351
	2002	0.027	0.0161	0.0454	0.023	0.0139	0.0380
	2003	0.068	0.0484	0.0938	0.058	0.0420	0.0793
	2004	0.042	0.0297	0.0593	0.036	0.0258	0.0495
	2005	0.066	0.0478	0.0903	0.056	0.0419	0.0757
	2006	0.049	0.0351	0.0667	0.041	0.0311	0.0550
CO3	1996	0.000	0.0000	1.0000			
	1997	0.022	0.0078	0.0618	0.019	0.0066	0.0524
	1998	0.003	0.0003	0.0192	0.002	0.0003	0.0162
	1999	0.043	0.0222	0.0814	0.037	0.0194	0.0681
	2000	0.047	0.0253	0.0859	0.040	0.0218	0.0727
	2001	0.064	0.0372	0.1093	0.055	0.0315	0.0945
	2002	0.015	0.0079	0.0294	0.013	0.0068	0.0246
	2003	0.039	0.0221	0.0672	0.033	0.0190	0.0568
	2004	0.024	0.0134	0.0421	0.020	0.0115	0.0353
	2005	0.038	0.0216	0.0654	0.032	0.0187	0.0550
	2006	0.028	0.0157	0.0481	0.023	0.0136	0.0400
GU2	1996	0.000	0.0000	1.0000			
	1997	0.020	0.0076	0.0495	0.017	0.0065	0.0420
	1998	0.002	0.0003	0.0160	0.002	0.0003	0.0135
	1999	0.038	0.0232	0.0618	0.032	0.0204	0.0513
	2000	0.042	0.0260	0.0662	0.036	0.0224	0.0560
	2001	0.057	0.0386	0.0841	0.049	0.0324	0.0730
	2002	0.013	0.0079	0.0228	0.011	0.0068	0.0191
	2003	0.034	0.0231	0.0509	0.029	0.0198	0.0429
	2004	0.021	0.0139	0.0318	0.018	0.0120	0.0266
	2005	0.033	0.0224	0.0496	0.028	0.0194	0.0416
	2006	0.024	0.0163	0.0364	0.021	0.0142	0.0302
GR1	1996	0.000	0.0000	1.0000			
	1997	0.046	0.0178	0.1147	0.039	0.0152	0.0984
	1998	0.005	0.0007	0.0385	0.005	0.0006	0.0326
	1999	0.087	0.0531	0.1406	0.075	0.0466	0.1186
	2000	0.095	0.0600	0.1482	0.082	0.0519	0.1270
	2001	0.128	0.0879	0.1829	0.111	0.0746	0.1611
	2002	0.032	0.0185	0.0548	0.027	0.0160	0.0460
	2003	0.079	0.0543	0.1142	0.068	0.0469	0.0974
	2004	0.049	0.0339	0.0716	0.042	0.0294	0.0602
	2005	0.077	0.0548	0.1080	0.066	0.0477	0.0912
	2006	0.057	0.0405	0.0798	0.049	0.0356	0.0664
GR3	1996	0.000	0.0000	1.0000			
	1997	0.032	0.0124	0.0798	0.027	0.0106	0.0681
	1998	0.004	0.0005	0.0264	0.003	0.0004	0.0223
	1999	0.061	0.0377	0.0976	0.052	0.0331	0.0817
	2000	0.067	0.0427	0.1031	0.057	0.0369	0.0878
	2001	0.091	0.0632	0.1289	0.078	0.0532	0.1129
	2002	0.022	0.0129	0.0372	0.019	0.0111	0.0312
	2003	0.055	0.0383	0.0792	0.047	0.0330	0.0672
	2004	0.034	0.0235	0.0494	0.029	0.0204	0.0414
	2005	0.054	0.0383	0.0753	0.046	0.0333	0.0634
	2006	0.039	0.0281	0.0553	0.034	0.0246	0.0458

Table 9. Mean distances traveled, time elapsed, and rate of travel per leg of movements made by stocked razorback suckers in the Upper Colorado River Basin, Utah and Colorado, 1995 – 2006.

leg		distance (RK)			time (d)			rate (RK/d)		
		mean	min	max	mean	min	max	mean	min	max
stocking to capture 1	(*n* = 2501)	58.9	0	514.9	261.6	0	3,164	0.93	0	55.37
capture 1 to capture 2	(*n* = 215)	11.5	0	194.2	179.1	1	1,799	0.44	0	8.50
capture 2 to capture 3	(*n* = 28)	9.4	0	44.5	103.1	1	1171	0.67	0	11.80
capture 3 to capture 4	(*n* = 3)	11.9	0	30.4	132.7	1	279	0.05	0	0.11

Table 10. Movements of hatchery-reared razorback suckers from stocking reach to any subsequent recapture reach in the Upper Colorado River Basin, Utah and Colorado. Percentages of total movements from initial reach are in parentheses. CO1 = Colorado River, RK 0.0 – 200.0; CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; CO3 = Colorado River, RK 303.3 – 390.0; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0; GR2 = Green River, RK 206.1 – 347.7; GR3 = Green River, RK 347.8 – 540.0; SR = San Rafael, tributary at Green River RK 156.2; DU = Duchesne River, tributary at Green River RK 399.3; WH = White River, tributary at Green River RK 396.7.

stocking reach	recapture reach										
	CO3	CO2	CO1	GU2	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%)	1388
GR2											
GR1			6 (2%)			2 (1%)	268 (97%)				276
DU											
WH											
SR											
total		774	308	92	1245	76	320	14	9	1	2839

Table 11. Movements of hatchery-reared razorback suckers between any two reaches on a leg, regardless of stocking reach, in the Upper Colorado River Basin, Utah and Colorado, 1995–2006. Percentages of total movements from initial reach are in parentheses. CO1 = Colorado River, RK 0.0 – 200.0; CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; CO3 = Colorado River, RK 303.3 – 390.0; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0; GR2 = Green River, RK 206.1 – 347.7; GR3 = Green River, RK 347.8 – 540.0; SR = San Rafael, tributary at Green River RK 156.2; DU = Duchesne River, tributary at Green River RK 399.3; WH = White River, tributary at Green River RK 396.7.

from reach	to reach										
	CO3	CO2	CO1	GU2	GR3	GR2	GR1	DU	WH	SR	total
CO3		26 (87%)	4 (13%)								30
CO2		662 (72%)	254 (28%)	1 (<1%)			2 (<1%)				917
CO1			24 (96%)				1 (4%)				25
GU2		86 (43%)	18 (9%)	91 (45%)			6 (3%)				201
GR3			2 (<1%)		1239 (90%)	70 (5%)	37 (3%)	15 (1%)	9 (<1%)	1 (<1%)	1373
GR2					1 (20%)	4 (80%)					5
GR1			6 (2%)			2 (1%)	273 (97%)				281
DU					4 (100%)						4
WH					1 (100%)						1
SR											
total		774	308	92	1245	76	319	15	9	1	2839

Table 12. Mean distances traveled (RK) and rates of travel (RK/d) between captures of razorback suckers stocked in winter (November and December), spring (March, April, and May), summer (June, July, and August), and autumn (September and October), 1995 – 2006, in the Upper Colorado River Basin, Utah and Colorado.

leg	stocking season							
	winter		spring		summer		autumn	
	RK	RK/d	RK	RK/d	RK	RK/d	RK	RK/d
stocking to capture 1	95.5	0.37	53.5	1.24	40.1	1.29	65.4	0.61
capture 1 to capture 2	10.4	0.96	7.8	0.46	14.9	2.00	14.5	0.34
capture 2 to capture 3	27.5	0.45	2.5	0.21	2.1	0.30	16.9	1.45
capture 3 to capture 4			0.0	0.00			17.8	0.08
overall	86.7	0.42	48.9	1.16	38.3	1.34	61.0	0.59

Table 13. Mean distance traveled, time elapsed, and rate of travel between stocking to 1st recapture of razorback suckers stocked into reaches of varying lengths in the Upper Colorado River Basin, Utah and Colorado, 1995 – 2006. CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; CO3 = Colorado River, RK 303.3 – 390.0; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0; GR3 = Green River, RK 347.8 – 540.0.

stocking reach	reach length (RK)	mean distance (RK)	mean time (d)	mean rate (RK/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

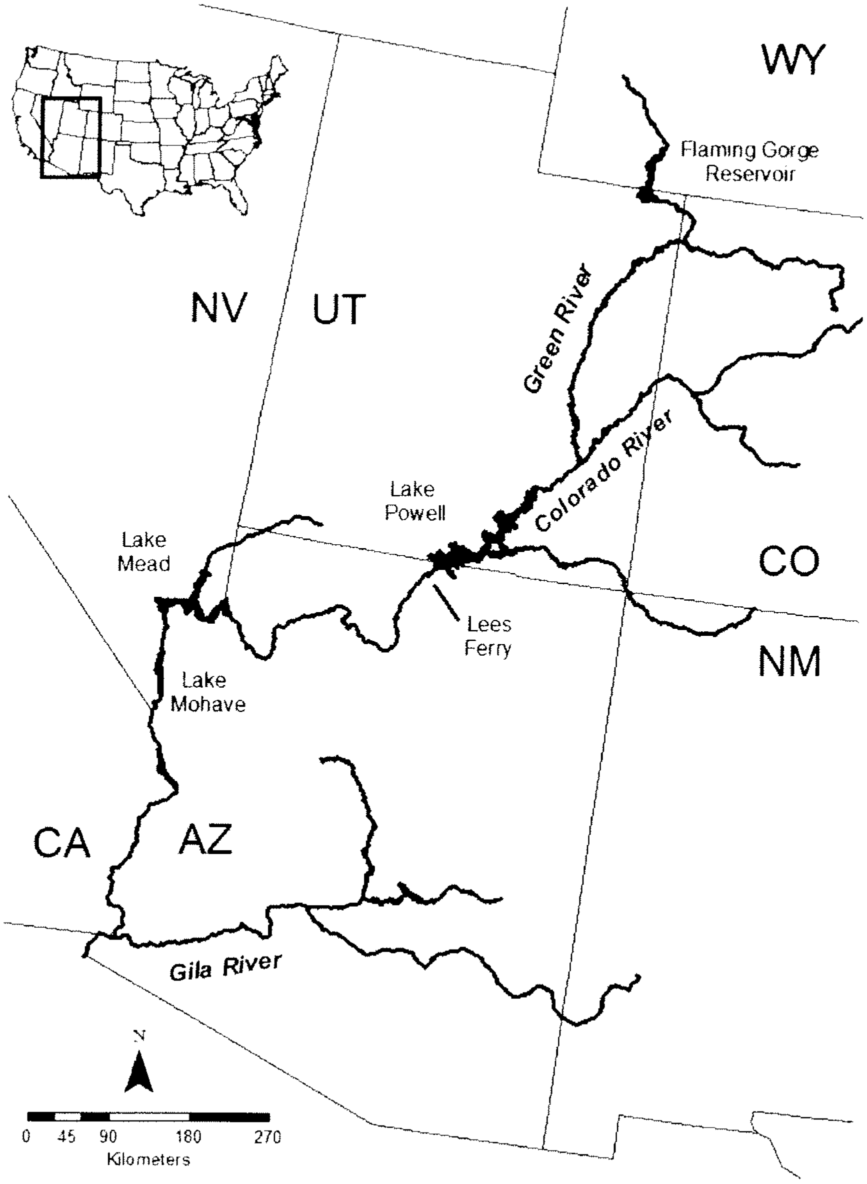

Figure 1. Map of the Colorado River Basin. Lees Ferry divides the Upper and Lower Colorado River basins.

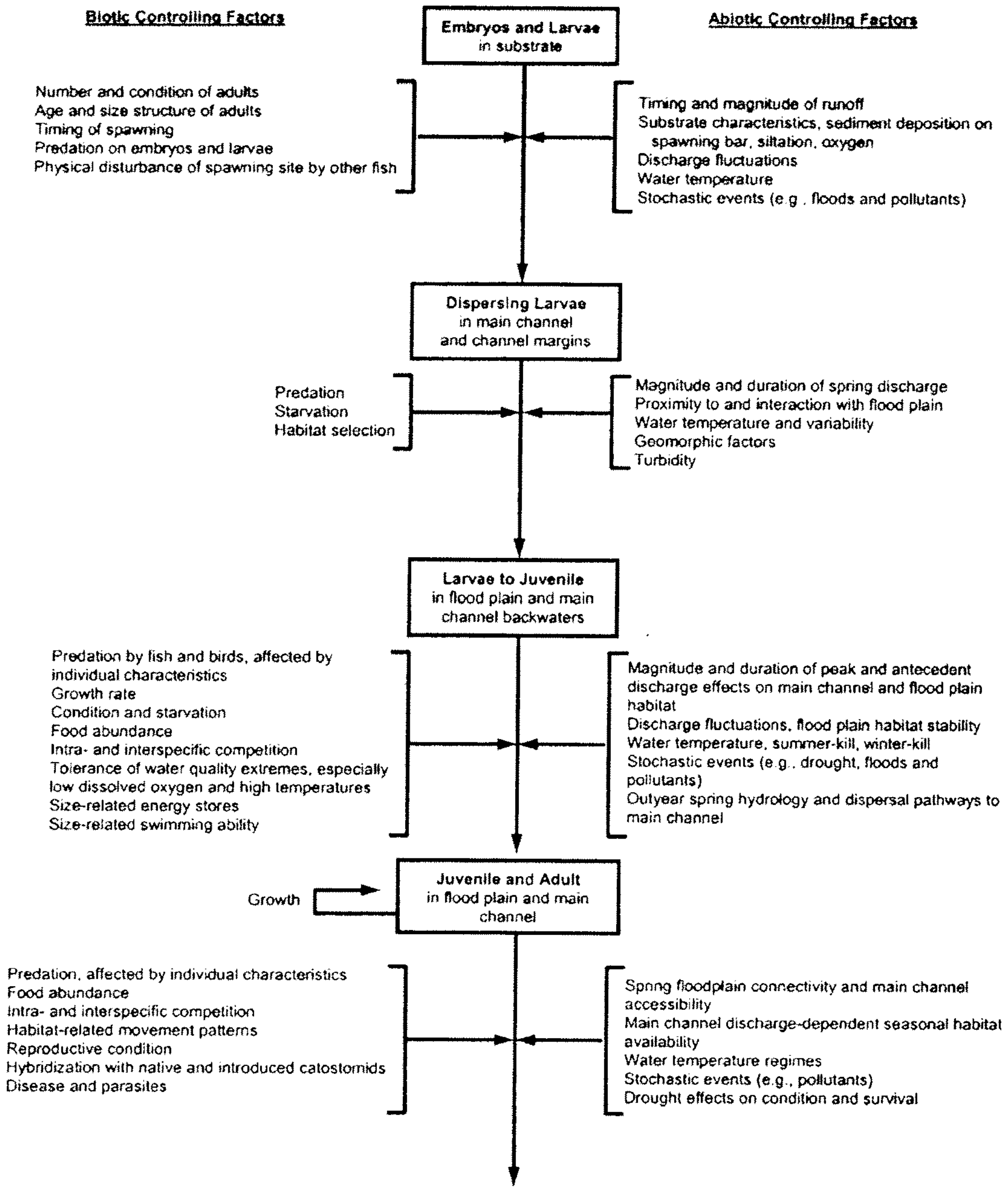

Figure 2. Razorback sucker life history conceptual model (Bestgen et al. 2007b).

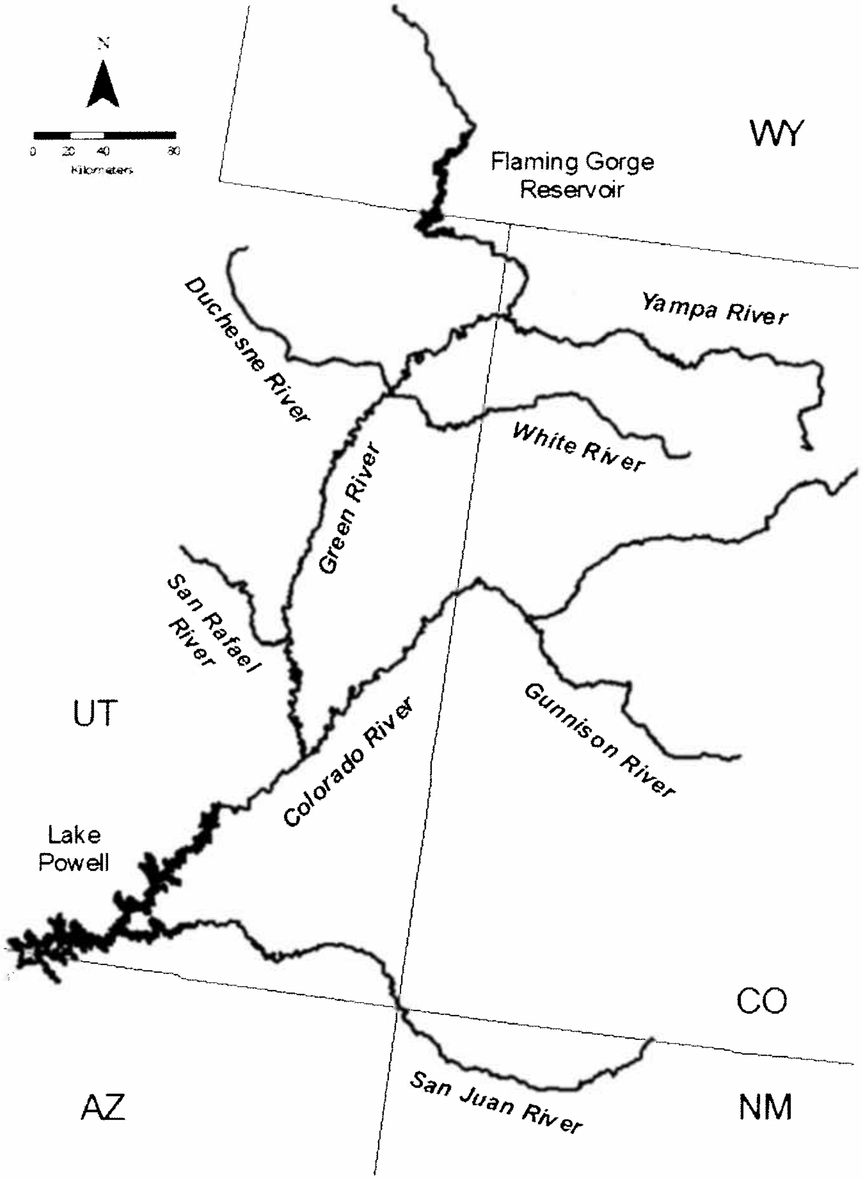

Figure 3. Map of the Upper Colorado River Basin.

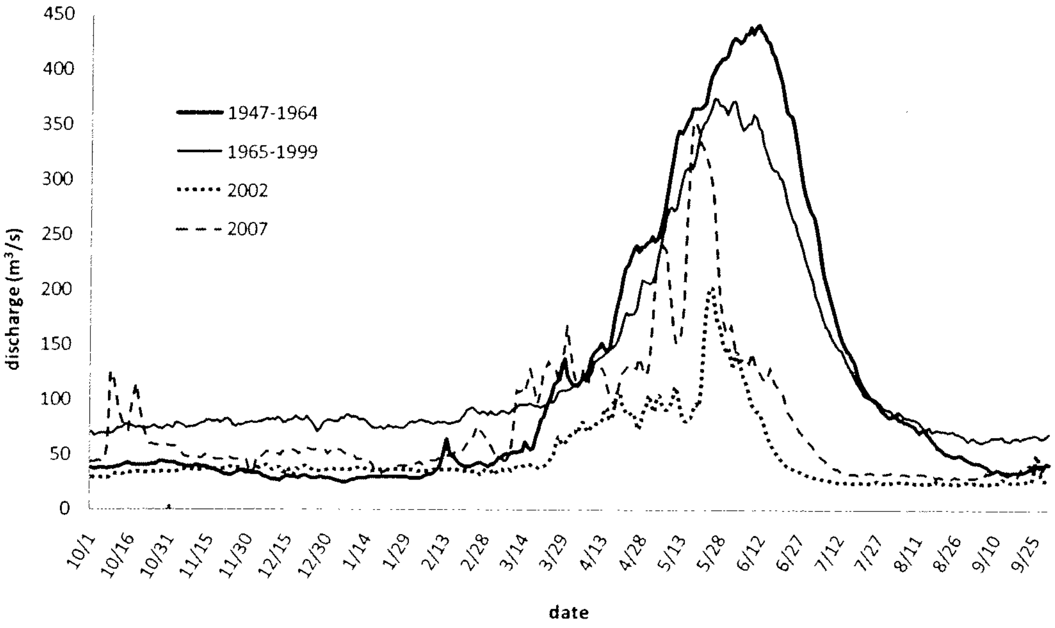

Figure 4. Mean daily discharge of the Green River near Jensen, Utah (U.S. Geological Survey gage 09261000), for water years 1947–1964, 1965–1999, 2002, and 2007.

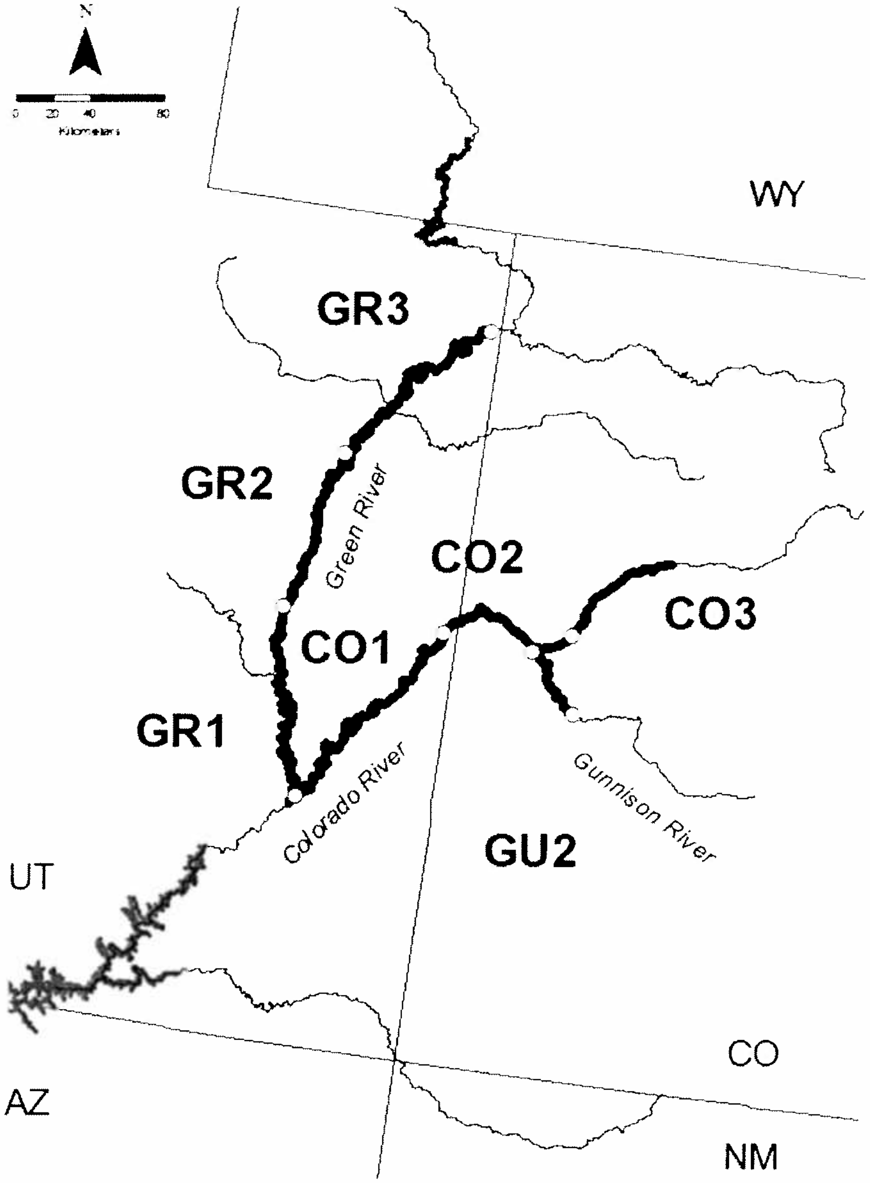

Figure 5. Study reaches within the Upper Colorado River Basin. CO1 = Colorado River, RK 0.0 – 200.0; CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; CO3 = Colorado River, RK 303.3 – 390.0; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0; GR2 = Green River, RK 206.1 – 347.7; GR3 = Green River, RK 347.8 – 540.0. Open circles denote reach boundaries.

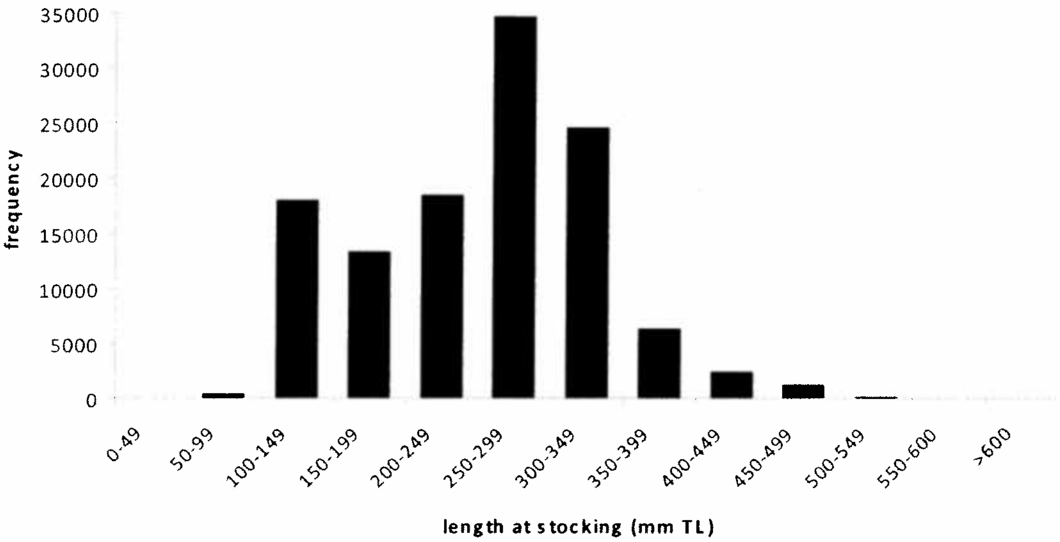

Figure 6. Length frequency of razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 1995–2005.

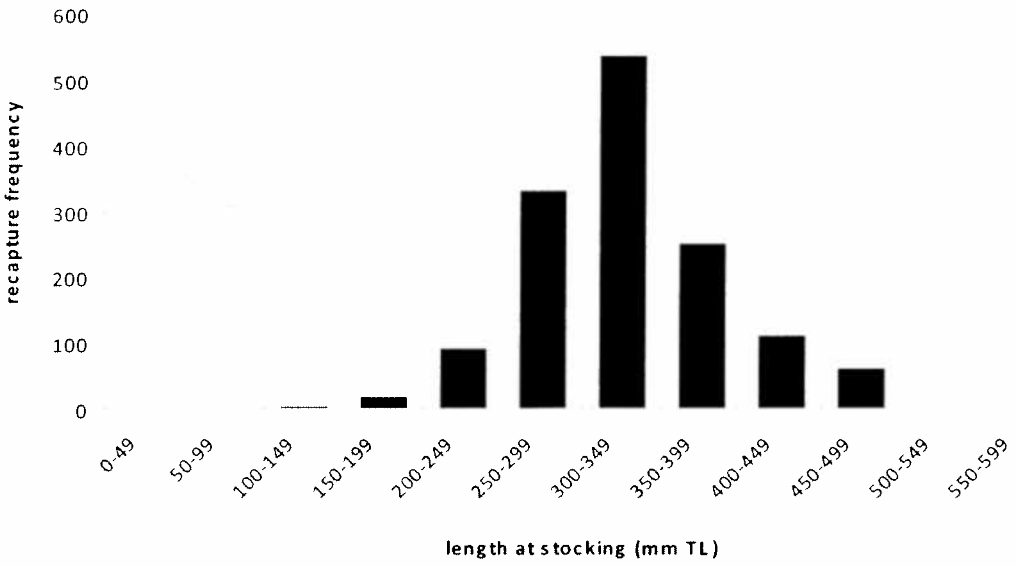

Figure 7. Length frequency of razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 1995–2005, and subsequently recaptured, 1996–2006.

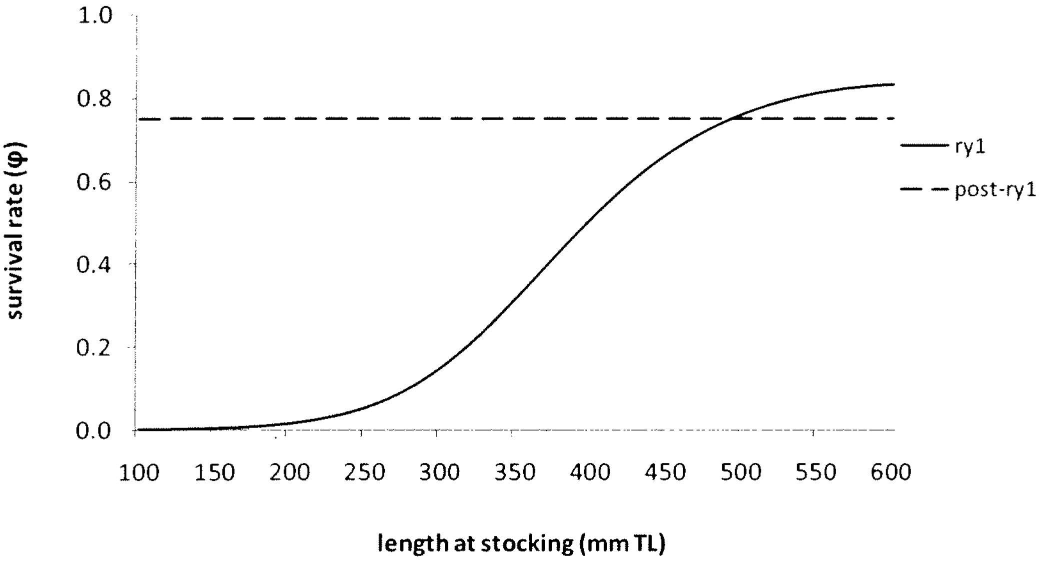

Figure 8. 1st-interval (ry1) and subsequent-interval (post-ry1) survival rate (φ) estimates, averaging over stocking season, for razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 1995–2005. The arrow indicates 1st-interval survival rate estimate for a razorback sucker of average length at stocking (252.5 mm TL).

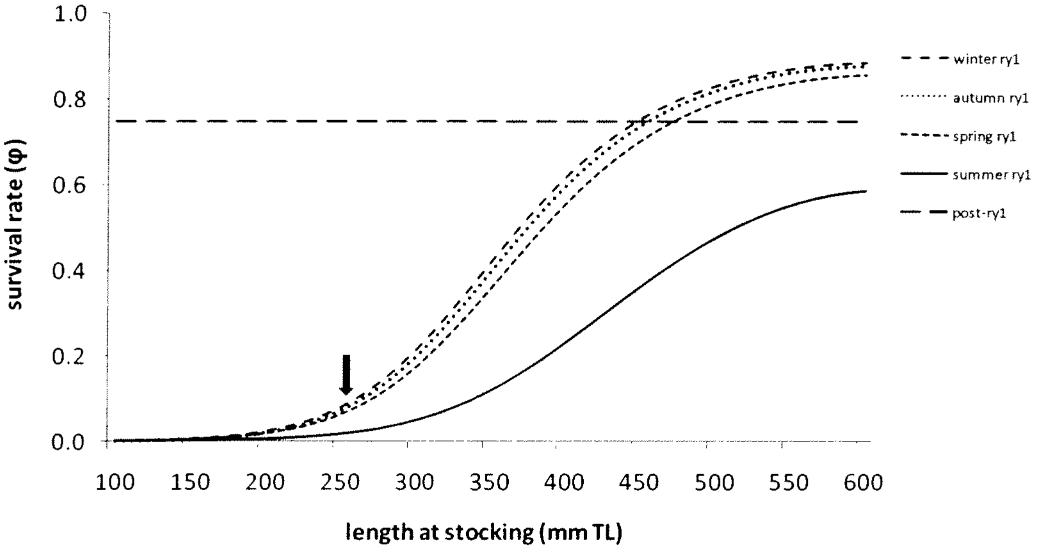

Figure 9. 1st-interval (ry1) survival rate (φ) estimates per stocking season compared to subsequent-interval (post-ry1) estimates for razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 1995–2005. Winter = November and December; spring = March, April, and May; summer = June, July, and August; autumn = September and October. The arrow indicates 1st-interval survival rate estimate for a razorback sucker of average length at stocking (252.5 mm TL).

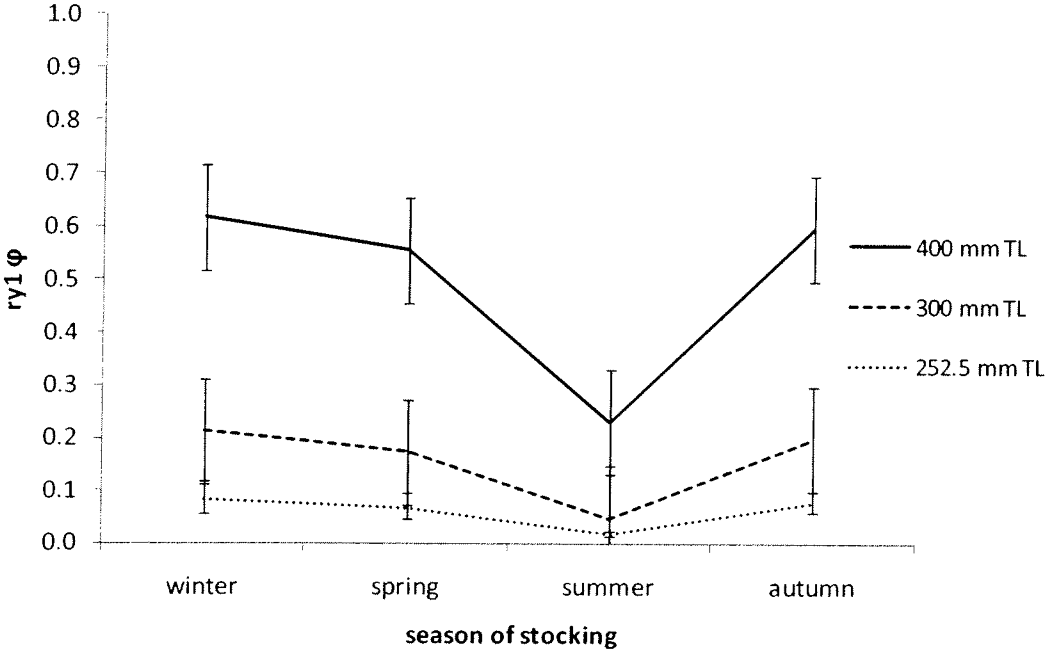

Figure 10. Predicted 1st-interval survival rate (ry1 φ) estimates for 252.5, 300, and 400 mm TL razorback suckers stocked during winter, spring, summer, and autumn into the Upper Colorado River Basin, Utah and Colorado, 1995–2005. Winter = November and December; spring = March, April, and May; summer = June, July, and August; autumn = September and October. 252.5 mm TL = average length at stocking, 300 mm TL = recommended length at stocking (Nesler et al. 2003), 400 mm TL = adult razorback sucker.

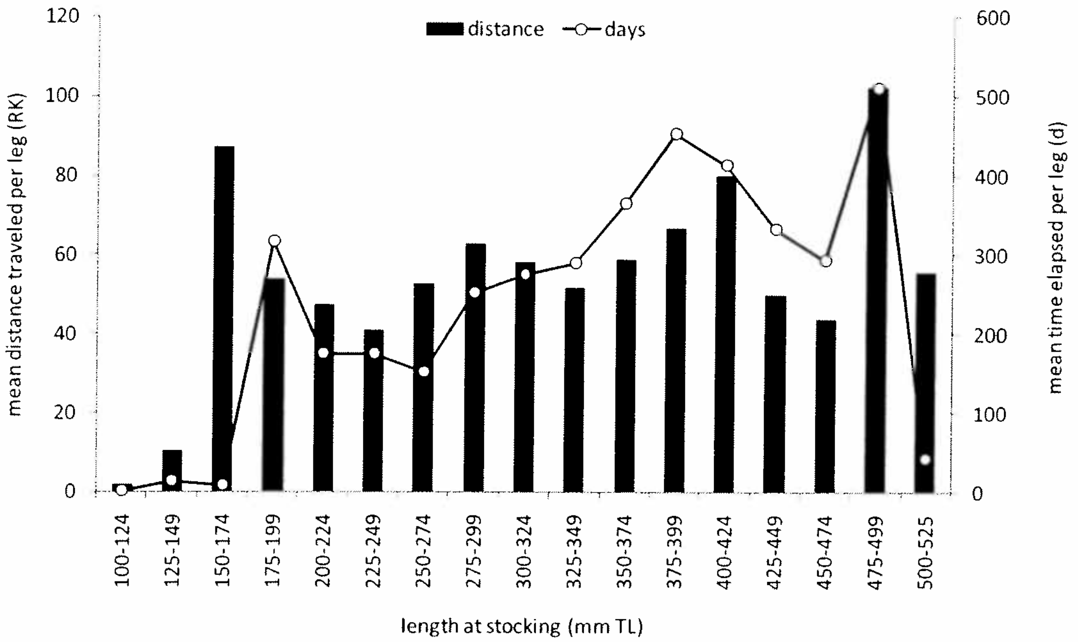

Figure 11. Mean distance traveled (RK) and mean time elapsed (d) per leg (from stocking or capture to next recapture) of movements made by razorback suckers of varying lengths at stocking in the Upper Colorado River Basin, Utah and Colorado, 1995–2006.

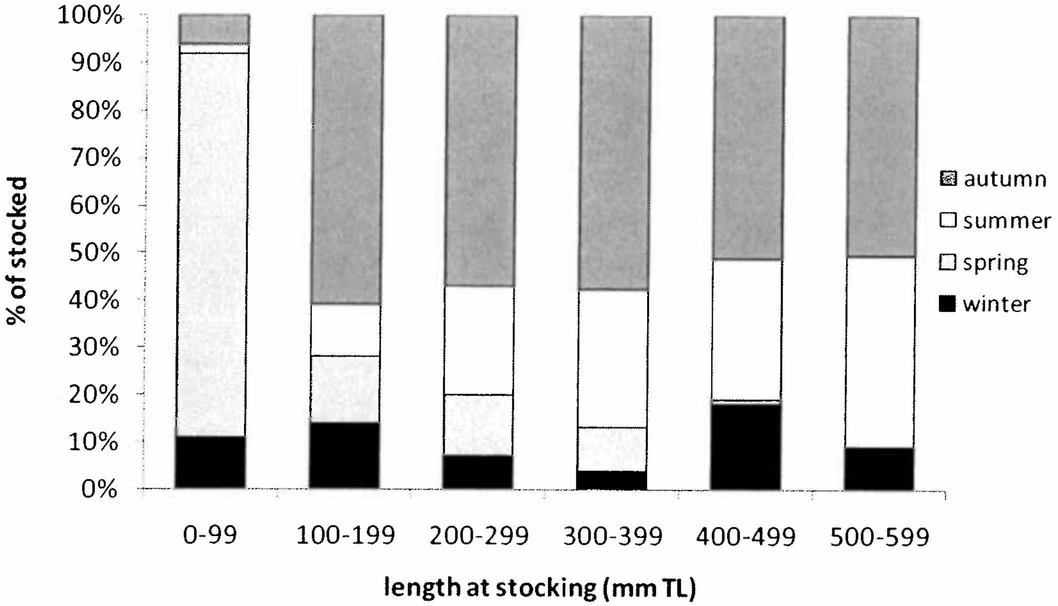

Figure 12. Percentages of total length ranges stocked in winter, spring, summer, and autumn for razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado. Winter = November and December; spring = March, April, and May; summer = June, July, and August; autumn = September and October.

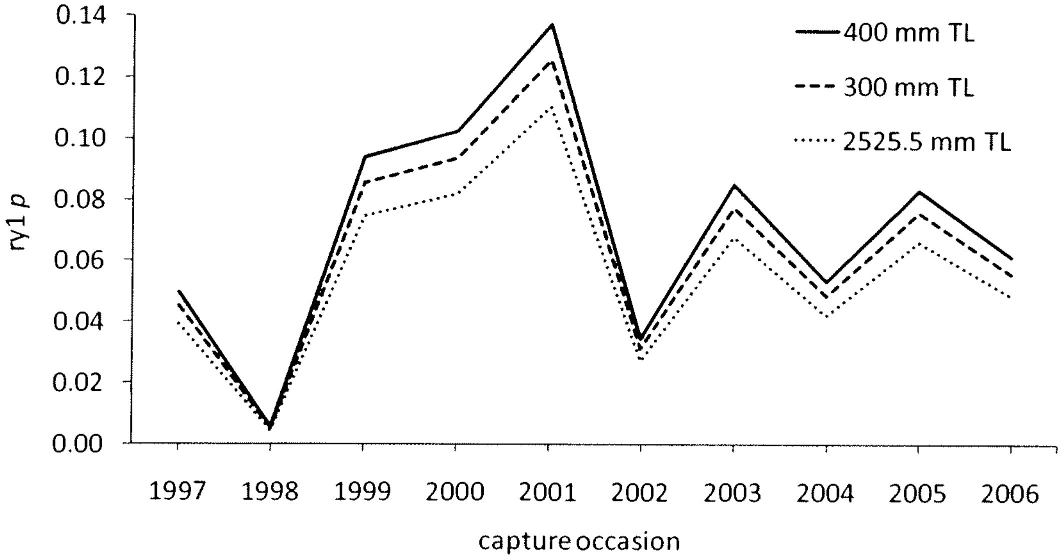

Figure 13. 1st-occasion capture probability estimates (ry1 *p*), 1997–2006, for 252.5, 300, and 400 mm TL razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado. 252.5 mm TL = average length at stocking, 300 mm TL = recommended length at stocking (Nesler et al. 2003), 400 mm TL = adult razorback sucker.

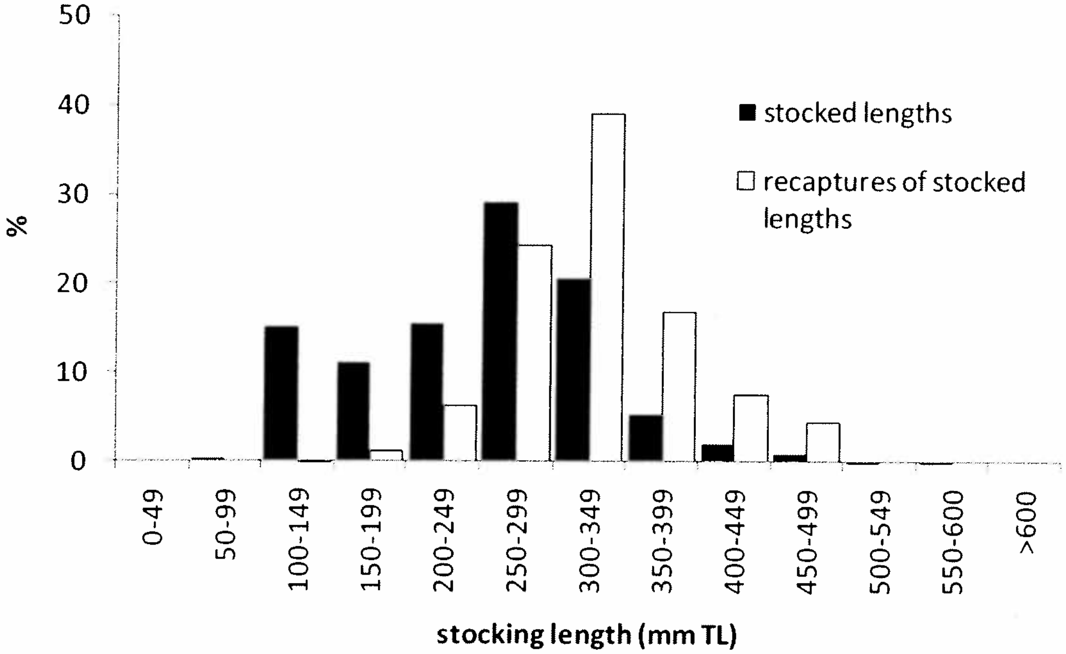

Figure 14. Length frequency as percent of fish stocked and as percent of fish stocked and subsequently recaptured for razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 1995–2005.

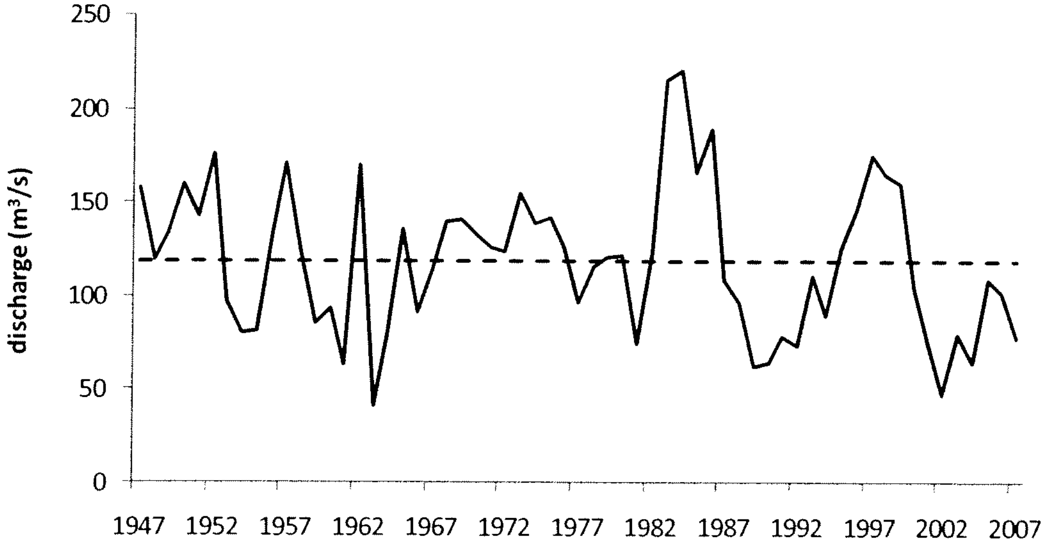

Figure 15. Mean annual discharge of the Green River near Jensen, Utah (U.S. Geological Survey gage 09261000), for water years1947 through 2007. The dashed line represents mean discharge for the entire period.

APPENDIX A:

MODEL STRUCTURES TO ESTIMATE APPARENT SURVIVAL AND CAPTURE PROBABILITY FOR RAZORBACK SUCKERS STOCKED INTO THE UPPER COLORADO RIVER BASIN, UTAH AND COLORADO, 1995–2005.

Appendix A. A priori model structures to estimate apparent survival, φ, and capture probability, p, for razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 1995–2005. Effects included: no variation (.), group or stocking reach (*g*), time (*t*), 1st interval or occasion in the river (ry1), stocking season (season), total length at stocking (TL, TL^2, TL^3), and sampling effort (eff).

φ	p structures
$\varphi\ (.)$	$p\ (.)$
$\varphi\ (g)$	$p\ (g)$
$\varphi\ (t)$	$p\ (t)$
$\varphi\ (\mathrm{ry1})$	$p\ (\mathrm{ry1})$
$\varphi\ (\mathrm{ry1} + \mathrm{TL})$	$p\ (\mathrm{ry1} + \mathrm{TL})$
$\varphi\ (\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2)$	$p\ (\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2)$
$\varphi\ (\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3)$	$p\ (\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3)$
$\varphi\ (\mathrm{ry1} + \mathrm{season})$	$p\ (g + t)$
$\varphi\ (g + t)$	$p\ (g + \mathrm{ry1})$
$\varphi\ (g + \mathrm{ry1})$	$p\ (g + [\mathrm{ry1} + \mathrm{TL}])$
$\varphi\ (g + [\mathrm{ry1} + \mathrm{TL}])$	$p\ (g + [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2])$
$\varphi\ (g + [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2])$	$p\ (g + [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3])$
$\varphi\ (g + [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3])$	$p\ (\mathrm{ry1} + t)$
$\varphi\ (g + [\mathrm{ry1} + \mathrm{season}])$	$p\ (\mathrm{ry1} + \mathrm{TL} + t)$
$\varphi\ (\mathrm{ry1} + t)$	$p\ (\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + t)$
$\varphi\ (\mathrm{ry1} + \mathrm{TL} + t)$	$p\ (\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3 + t)$
$\varphi\ (\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + t)$	$p\ (g + [\mathrm{ry1} + t])$
$\varphi\ (\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3 + t)$	$p\ (g + [\mathrm{ry1} + \mathrm{TL} + t])$
$\varphi\ (\mathrm{ry1} + \mathrm{season} + \mathrm{TL})$	$p\ (g + [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + t])$
$\varphi\ (\mathrm{ry1} + \mathrm{season} + \mathrm{TL} + \mathrm{TL}^2)$	$p\ (g + [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3 + t])$
$\varphi\ (\mathrm{ry1} + \mathrm{season} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3)$	$p\ (g + \mathrm{eff})$
$\varphi\ (\mathrm{ry1} + \mathrm{season} + t)$	$p\ (g + \mathrm{eff} + \mathrm{ry1})$
$\varphi\ (g + [\mathrm{ry1} + t])$	$p\ (g + \mathrm{eff} + [\mathrm{ry1} + \mathrm{TL}])$
$\varphi\ (g + [\mathrm{ry1} + \mathrm{TL} + t])$	$p\ (g + \mathrm{eff} + [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2])$
$\varphi\ (g + [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + t])$	$p\ (g + \mathrm{eff} + [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3])$
$\varphi\ (g + [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3 + t])$	$p\ (g * t)$
$\varphi\ (g + [\mathrm{ry1} + \mathrm{season} + t])$	$p\ (g * \mathrm{ry1})$
$\varphi\ (\mathrm{ry1} + \mathrm{season} + \mathrm{TL} + t)$	$p\ (g * [\mathrm{ry1} + \mathrm{TL}])$
$\varphi\ (\mathrm{ry1} + \mathrm{season} + \mathrm{TL} + \mathrm{TL}^2 + t)$	$p\ (g * [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2])$
$\varphi\ (\mathrm{ry1} + \mathrm{season} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3 + t)$	$p\ (g * [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3])$
$\varphi\ (g + [\mathrm{ry1} + \mathrm{season} + \mathrm{TL} + t])$	$p\ (g * [\mathrm{ry1} + \mathrm{t}])$
$\varphi\ (g + [\mathrm{ry1} + \mathrm{season} + \mathrm{TL} + \mathrm{TL}^2 + t])$	$p\ (g * [\mathrm{ry1} + \mathrm{TL} + \mathrm{t}])$
$\varphi\ (g + [\mathrm{ry1} + \mathrm{season} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3 + t])$	$p\ (g * [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + t])$
$\varphi\ (g * t)$	$p\ (g * [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3 + t])$
$\varphi\ (g * \mathrm{ry1})$	
$\varphi\ (g * [\mathrm{ry1} + \mathrm{TL}])$	
$\varphi\ (g * [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2])$	
$\varphi\ (g * [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3])$	
$\varphi\ (g * [\mathrm{ry1} + \mathrm{season}])$	
$\varphi\ (g * [\mathrm{ry1} + t])$	
$\varphi\ (g * [\mathrm{ry1} + \mathrm{TL} + t])$	
$\varphi\ (g * [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + t])$	
$\varphi\ (g * [\mathrm{ry1} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3 + \mathrm{t}])$	
$\varphi\ (g * [\mathrm{ry1} + \mathrm{season} + t])$	
$\varphi\ (g * [\mathrm{ry1} + \mathrm{season} + \mathrm{TL} + t])$	
$\varphi\ (g * [\mathrm{ry1} + \mathrm{season} + \mathrm{TL} + \mathrm{TL}^2 + t])$	
$\varphi\ (g * [\mathrm{ry1} + \mathrm{season} + \mathrm{TL} + \mathrm{TL}^2 + \mathrm{TL}^3 + t])$	

APPENDIX B:

PROGRAM MARK RESULTS FOR MODELS TO ESTIMATE APPARENT SURVIVAL AND CAPTURE PROBABILITY FOR RAZORBACK SUCKERS STOCKED INTO THE UPPER COLORADO RIVER BASIN, UTAH AND COLORADO, 1995–2005.

Appendix B. Cormack-Jolly-Seber open population models to estimate apparent survival (φ) and capture probability (*p*) for hatchery-reared razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, from 1995 to 2005. Effects included: no variation (.), group or stocking reach (*g*), time (*t*), 1st interval or occasion in the river (ry1), stocking season (season), and total length at stocking (TL and TL^2).

Model	AIC$_c$	Delta AIC$_c$	AIC$_c$ Weights	Model Likelihood	Number of Parameters	Deviance
{φ(ry1+season+TL+TL^2) *p*(*g*+[ry1+TL+TL^2+*t*]))	15614.582	0	0.994	1.000	24	15566.582
{φ(ry1+season+TL+TL^2) *p*(*g*+*t*))	15624.877	10.295	0.006	0.006	21	15582.877
{φ(ry1+TL+TL^2) *p*(*g*+[ry1+TL+TL^2+*t*])}	15839.803	225.221	0	0	21	15797.803
{φ(*g*+[ry1+TL+TL^2]) *p*(*g*+[ry1+TL+TL^2+*t*]))	15843.270	228.688	0	0	25	15793.270
{φ(ry1+TL+TL^2) *p*(*g*+[ry1+*t*]))	15844.069	229.487	0	0	19	15806.069
{φ(*g*+[ry1+TL+TL^2]) *p*(*g*+[ry1+*t*])}	15845.244	230.662	0	0	23	15799.244
{φ(*g*+[ry1+TL+TL^2]) *p*(*g*+*t*)}	15850.340	235.758	0	0	22	15806.340
{φ(ry1+TL+TL^2) *p*(*g*+*t*))	15854.285	239.703	0	0	18	15818.285
{φ(ry1+TL+TL^2) *p*(*t*)}	15911.444	296.862	0	0	14	15883.444
{φ(ry1+TL+TL^2) *p*(*g*+ry1))	15941.134	326.552	0	0	10	15921.134
{φ(*g*+[ry1+TL+TL^2]) *p*(*g*+[ry1+TL+TL^2])}	15943.869	329.287	0	0	16	15911.869
{φ(ry1+TL+TL^2) *p*(*g*))	15957.927	343.345	0	0	9	15939.927
{φ(*g*+[ry1+TL+TL^2]) *p*( ))	15987.018	372.436	0	0	9	15969.018
{φ(*g*+[ry1+TL]) *p*( )}	15999.770	385.188	0	0	8	15983.770
{φ(ry1+TL+TL^2) *p*(ry1))	16007.392	392.810	0	0	6	15995.392
{φ(ry1+TL+TL^2) *p*( )}	16023.566	408.984	0	0	5	16013.566
{φ(ry1+TL) *p*( )}	16033.348	418.766	0	0	4	16025.348
{φ(*g*+[TL+TL^2]) *p*(*g*+[TL+TL^2])logit}	16037.381	422.799	0	0	14	16009.381
{φ(*g*+[TL+TL^2]) *p*( )}	16097.012	482.430	0	0	8	16081.012
{φ(TL+TL^2) *p*(.)}	16115.232	500.650	0	0	4	16107.232
{φ(g*season) *p*(*g*+[ry1+TL+TL^2+*t*]))	16144.052	529.470	0	0	29	16086.052
{φ(ry1+TL+TL^{2}all) *p*( ) productTL,TL}	16191.468	576.886	0	0	5	16181.468
{φ(ry1+TL+TL^{2}all) *p*( )}	16191.468	576.886	0	0	5	16181.468
{φ(*g*+season) *p*(*g*+[ry1+TL+TL^2+*t*])}	16206.099	591.517	0	0	24	16158.099
{φ(ry1+season) *p*(*g*+[ry1+TL+TL^2+*t*]))	16238.644	624.062	0	0	22	16194.644
{φ(ry1+TLall) *p*(.))	16252.344	637.762	0	0	4	16244.344
{φ(season) *p*(*g*+[ry1+TL+TL^2+*t*])}	16264.086	649.504	0	0	21	16222.086
{φ(TL+TL^2) *p*(.)stndz}	16395.929	781.347	0	0	4	16387.929
{φ(*g*+[TL+TL^2]) *p*( )stndz)	16400.724	786.142	0	0	8	16384.724
{φ(.) *p*{*g*+[ry1+TL+TL^2])}	16594.500	979.918	0	0	9	16576.500
{φ(.) *p*(*g*+[ry1+TL])}	16644.417	1029.835	0	0	8	16628.417
{φ(*g*+ry1) *p*(*g*+t)}	16897.446	1282.864	0	0	20	16857.446
{φ(ry1) *p*(*g*+*t*)}	16920.327	1305.745	0	0	16	16888.327
{φ(*g*) *p*(*g*+*t*)}	16953.750	1339.168	0	0	19	16915.750
{φ(*g*+ry1) *p*(*t*)}	16970.352	1355.770	0	0	16	16938.352
{φ(.) *p*(*g*+*t*))	16989.831	1375.249	0	0	15	16959.831
{φ(.) *p*(*g*+[ry1+*t*]))	16990.834	1376.252	0	0	16	16958.834
{φ(*g*) *p*(*t*))	17053.820	1439.238	0	0	15	17023.820
{φ(ry1) *p*(*t*)}	17101.375	1486.793	0	0	12	17077.375
{φ(*g*+ry1) *p*(*g*+ry1)}	17110.362	1495.780	0	0	12	17086.362
{φ(*g*+ry1) *p*(*g*)}	17117.598	1503.016	0	0	11	17095.598
{φ(ry1) *p*(*g*+ry1))	17136.993	1522.411	0	0	8	17120.993
{φ(ry1) *p*(*g*))	17152.198	1537.616	0	0	7	17138.198
{φ( ) *p*(*t*)}	17159.631	1545.049	0	0	11	17137.631
{φ(*g*) *p*(*g*))	17190.434	1575.852	0	0	10	17170.434
{φ(*g*) *p*(*g*)278 fixed to 0}	17190.434	1575.852	0	0	10	17170.434
{φ(*g*) *p*(*g*+ry1))	17192.182	1577.600	0	0	11	17170.182
{φ(*g*+ry1) *p*(ry1)}	17219.215	1604.633	0	0	8	17203.215
{φ(.) *p*(*g*+ry1))	17239.209	1624.627	0	0	7	17225.209
{φ( ) *p*(*g*))	17241.615	1627.033	0	0	6	17229.615
{φ(*g*+ry1) *p*( )}	17270.169	1655.587	0	0	7	17256.169
{φ(*g*) *p*(ry1)}	17419.163	1804.581	0	0	7	17405.163
{φ(*g*) *p*(.)}	17427.094	1812.512	0	0	6	17415.094
{φ(ry1) *p*(ry1))	17729.466	2114.884	0	0	4	17721.466
{φ(ry1) *p*(.)}	17742.879	2128.297	0	0	3	17736.879
{φ( ) *p*(.)}	17833.716	2219.134	0	0	2	17829.716
{φ(.) *p*(ry1)}	17833.954	2219.372	0	0	3	17827.954