SURVIVAL RATE ESTIMATION OF HATCHERY-REARED RAZORBACK SUCKERS *XYRAUCHEN TEXANUS* STOCKED IN THE UPPER COLORADO RIVER BASIN, UTAH AND COLORADO, 2004–2007

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EXECUTIVE SUMMARY

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 before downlisting or delisting can occur. Current wild populations are so depleted that the first management action to achieve recovery is to reestablish populations with hatchery-produced fish. An integrated stocking plan was implemented in 2003 and stocking goals initiated in 2004 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 which must become self-sustaining to meet recovery goals. The stocking plan assumes annual survival rates of 50% for age-2 fish, 60% for age-3 fish, and 70% for adult (≥ age-4) fish.

We used tag recapture data to estimate apparent survival, φ, and capture probability, *p*, for 96,448 hatchery-reared razorback suckers stocked into Upper Colorado River Basin streams, 2004–2007. Annual recapture data included 1,511 recapture events of 1,470 individuals from 2005–2008. We investigated the following effects: rearing method, reach, year, and season of stocking, fish total length (TL) at time of stocking, and first year in the river after stocking versus subsequent years. Mean first-year survival rates for razorback suckers of average TL (301.5 mm) stocked from 2005–2007 were low for fish reared by all methods: 0.03, 0.05, and 0.08 for tank-, pond-, and intensively (combination of indoor tank and outdoor pond)-reared fish, respectively. Rates were higher in the 2004–2005 interval for pond-reared (0.20) and intensively-reared (0.27) razorback suckers; no tank-reared fish were stocked that year. Total length at stocking and 1st-year survival were positively correlated; survival of fish (reared

by any method) smaller than 200 mm TL approached zero but increased to an average of 0.83 for the few fish larger than 500 mm TL. Mean 1st-year survival of razorback suckers of average total length at stocking (301.5 mm) was 0.09. Season of stocking had a large effect on razorback sucker 1st-year survival rate estimates. Mean rates for razorback suckers of average TL (301.5 mm) stocked during summer were 0.03, 0.03, and 0.04 for tank-, pond-, and intensively-reared fish, respectively. Stocking during spring produced the highest mean estimates: 0.20, and 0.29 for pond-, and intensively-reared fish, respectively. Only five tank-reared razorback suckers were stocked during spring, none of which were recaptured during the study period. Effects of tank-rearing and summer-stocking could not be distinguished, since nearly all tank-reared fish (94%) were stocked during summer months. However, the adverse effect of stocking during summer was demonstrated by similar, low 1st-interval survival of fish reared by other methods. Furthermore, proportions of summer-stocked individuals subsequently recaptured were 0.5% or lower for pond- and intensively-reared razorback suckers. Tank- and pond-reared razorback suckers had higher predicted 1st-interval survival when stocked into the lower Green River reach (GR1) than Colorado or Gunnison River reaches. Survival of intensively-reared fish did not differ among the Green River reaches. Comparisons among all rearing methods within reach GR1 were not possible due to imbalance of numbers stocked there per method and year. Survival rates for razorback suckers after their first intervals in the river were high: 0.75–0.94, depending on interval and rearing method. Capture probabilities were all low, ranging from an average of 0.10 for a fish (reared by any method) on its first occasion in the river after stocking down to 0.02 on subsequent occasions. Pond-reared razorback suckers were captured in the highest proportion (68% of all recaptures) and had the highest predicted recapture probabilities (0.11–0.31), when averaging across reaches and years of stocking.

Maintenance of self-sustaining populations is the underlying goal of all razorback sucker recovery efforts. Our 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 and predator-avoidance training, should be investigated further. A comprehensive razorback sucker monitoring program, which includes early life stages as well as adults, would assist with increasing recapture probabilities. Employing a standardized stocking protocol would allow better estimation of the effects of certain important variables, such as rearing methods. Implementation of management strategies derived from these post-stocking survival rate estimates will immediately enhance recovery prospects for razorback sucker in the Upper Colorado River Basin.

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KEY WORDS

Razorback sucker, Colorado River, hatchery, propagation, stocking plan, survival rate estimation, demographic parameters, endangered fishes, total length, season, non-native predators

INTRODUCTION

Demographic parameters that describe birth, movement, and mortality rates and population abundance are useful to understand status and dynamics of animal populations. Responses of populations to biotic or abiotic drivers are of interest to ecologists attempting to understand the fundamental basis for population change. They are also useful to managers attempting to maintain or enhance abundance of free-ranging and rare animal populations in need of conservation. 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 conservation 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, which began in the Upper Colorado River Basin (UCRB) in 1995. Survival rates for wild razorback suckers have been defined by previous studies (Modde et al. 1996; Bestgen et al. 2002), but were unknown for hatchery fish until recently. By analyzing mark-recapture data, Zelasko et al. (2009) estimated survival rates for hatchery-reared razorback suckers stocked into portions of the UCRB (Green and Colorado subbasins) from 1995–2005. However, in 2003 an updated, integrated stocking plan for razorback sucker was implemented (Nesler et al. 2003) and this study used mark-recapture data collected from 2004-2008 to refine the previous analysis.

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; Marsh et al. 2003). 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), wild razorback suckers were captured sporadically from the Colorado, 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 (Bestgen 1990; Minckley et al. 1991). 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 (Marsh et al. 2003; Albrecht et al. 2008). However, the once-large, wild population in Lake Mohave was recently estimated to number 24 fish (Kesner et al. 2010).

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 fish may have been 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 kilometers in length or more, historically occurred in spring in the UCRB to the Colorado River, lower Yampa River near its confluence with the Green River, and middle Green River between river kilometer (RK) 492 and 501 (Valdez et al. 1982; Osmundson and Kaeding 1989; Bestgen 1990; Tyus and Karp 1990; Osmundson and Seal 2009). 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). The exception is Lake Mead, where limited annual recruitment has been demonstrated through non-lethal aging techniques (Albrecht et al. 2008). However, 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 (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 are thought to influence survival of early life stages (Tyus 1987; Minckley et al. 1991; Mueller et al. 2003; Bestgen 2008). These factors, singly or synergistically, are thought to inhibit most 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 Basin 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 extirpation of razorback sucker. Therefore, the required self-sustaining populations can only be achieved with the aid of hatchery augmentation (U.S. Fish and Wildlife Service 2002), until sufficient recruitment is achieved and maintained.

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 each of 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, including stocking, 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 1997–2001, 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 summarized stocking and capture records throughout the basin from 1995–2005 (Francis and McAda 2006).

A thorough analysis of survival of hatchery-reared razorback suckers stocked from 1995–2005 was recently completed for a portion of the UCRB in the Green and Colorado River subbasins (Zelasko 2008; Zelasko et al. 2009). That analysis found survival through a fish's first interval in the river (stocking year to following sampling year) was considerably lower than rates assumed in the species' stocking plan: 0.05 (mean total length = 252.5 mm, averaging across season of stocking) vs. 0.50 (assumed for a similarly sized, age-2 fish). First-interval survival was positively related to total length at time of stocking, but razorback suckers of nearly all lengths survived at significantly lower rates when stocked during summer compared to any other season. After their first interval in the river, hatchery-reared razorback suckers survived at a rate similar to the adult rate assumed in the species' stocking plan (0.75 vs. 0.70). Data imbalances across stocking locations, years, and seasons left some combinations of those effects inestimable. However, stocking and recapture data collected from 2004–2008 under the species' integrated stocking plan (Nesler et al. 2003) will improve evaluation of both the plan and efforts aimed at re-establishing self-sustaining razorback sucker populations (U.S. Fish and Wildlife Service 2002).

Goal and objectives

The goal of this study was to provide an updated, basin-wide assessment of demographic parameter estimates for razorback suckers stocked in the Green and Colorado River basins since implementation of an integrated stocking plan, based on releases of hatchery-reared razorback suckers (2004–2007) and recapture data (2005–2008). Objectives to accomplish that goal were to:

1. compile and proof stocking and capture data for stocked razorback suckers,
2. identify covariates and effects 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 available in other parts of the range of razorback sucker and those assumed in stocking plans,
5. recommend revisions to stocking plans, based on results of analyses.

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

STUDY AREA

The Upper Colorado River Basin covers portions of Wyoming, Utah, Colorado, New Mexico, and Arizona (Figure 1). 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 valley 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 completion of Flaming Gorge Dam in 1964 in the upper Green River, Utah, spring peak flows of the Green River are lower and summer base flows are higher than historic levels. Recent low flow years have resulted in spring peaks with reduced duration and magnitude (Figure 2), a factor that may affect reproduction and recruitment of several UCRB endangered fish, including razorback sucker. The Shoshone power plant on the Colorado River, which began operations in 1909, and the Aspinall Unit (a series of three water storage and hydroelectric power dams) on the Gunnison River, which was authorized in 1956, have similarly altered flow regimes of those subbasins. However, flow recommendations intended to benefit endangered fishes in the UCRB, which would restore more natural base and spring peak flows to several rivers in the system, have either been implemented or are being formulated (Muth et al. 2000).

METHODS

Data

We obtained all data for this study from the centralized Upper Colorado River Basin database, created in Microsoft Access and maintained by USFWS, Grand Junction, Colorado. The database consisted of two components: hatchery release data for fish stocked directly into rivers and capture data from field sampling programs. Fish stocked into wetlands or floodplains for later connections to adjacent rivers were excluded from analyses, as they were not always available for capture during field sampling. The hatchery release data included: hatchery and rearing source, Passive Integrated Transponder (PIT) tag number, length (mm TL), weight (g), year class, lot number, and date and location of stocking. The capture data was collected under a variety of studies occurring in the UCRB, very few of which were specifically targeting the capture of razorback suckers. The data reported sampling agency and project, sampling gear, date, location, habitat type, recapture designation (Y/N), PIT tag number, and fish length, weight, sex, reproductive condition, and status (live or dead).

We 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. Compilation of the final data set for analysis consumed about three months of time by the senior author.

Groups

A primary interest in this study for the UCRB Recovery Program was the effect of propagation methods on razorback sucker survival. Therefore, we grouped all stocked fish by the method under which they were reared, as defined by hatchery personnel at each rearing facility. Stocked razorback suckers in this study were reared at two facilities: Grand Valley Endangered Fish Facility (GVEFF, USFWS, Grand Junction, Colorado) and Ouray National Fish Hatchery (ONFH, USFWS, Vernal, Utah). According to Travis Francis (USFWS, Grand Junction, personal communication), razorback suckers in this study were reared at GVEFF using three methods. Propagation began with rearing fish in the hatchery from incubation (April to May) until “grading” (May to August), at which time the smallest-graded fish ($n \approx$ 14,000–200,000+) were moved to outdoor rearing ponds until release (August to October of the following year). The ponds varied in size (surface acreage and depth) and consisted of leased or donated gravel pits as well as ponds built for fish culture. The gravel pits were utilized to condition fish to variable water conditions and natural diets, whereas the fish culture ponds were more controlled and supplemented with fish food pellets. The largest-graded fish (*n* ≈ 28,000) remained in the hatchery until the following spring (March to May), when most (n ≈ 21,000) moved to ponds until release (August to October) and the remainder (*n* ≈ 7,000) stayed in hatchery tanks until release (July to September). All fish were PIT-tagged prior to release.

Razorback suckers reared by the first two methods were often stocked into the same ponds and were not PIT-tagged until harvest and release. Since the two pond-rearing methods could not be distinguished after stocking, we grouped them into one method, labeled "pond": fish that spent any amount of time (approximately six months to one year) in outdoor rearing ponds. Those that were reared solely in hatchery tanks were labeled "tank".

According to Mike Montagne (USFWS, Vernal, personal communication), razorback suckers in this study were reared at ONFH by one method that alternated use of both hatchery tanks and ponds (labeled "intensive"). Upon swim-up, larvae were moved from hatchery tanks to outdoor ponds (with both natural food and supplemental pellets), where they remained until early autumn. Fish were then harvested and moved inside to hatchery tanks to increase over-winter growth. In spring, razorback suckers were returned to outdoor ponds, where they remained until harvest, PIT-tagging, and release in autumn.

Covariates

Database fields considered for inclusion in analyses were selected based on factors that may affect hatchery-reared razorback sucker survival and/or recapture probability, including: river reach, year, and season of stocking, fish TL, and fish weight. We designated data as individual or environmental, and continuous or categorical covariates.

Although river reaches where razorback suckers were stocked from 1995–2005 did not strongly affect survival when used as groups in our previous analysis, 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. As stocking protocols have become more consistent under the integrated stocking plan, estimation of razorback sucker survival rates per reach may be attainable. Therefore, we used previous studies (Osmundson and Burnham 1998; Osmundson et al. 1998; Bestgen et al. 2007a) and information about river gradient, geomorphology, and placement of diversions to divide the UCRB into seven river reaches (Figure 3) into which all stocking records would be arranged. Of those, five reaches received stocked fish on at least one occasion during the study period: CO2 (Colorado River from upstream of Westwater Canyon to Price-Stubb diversion, plus Gunnison River downstream of Redlands diversion), GU2 (Gunnison River upstream of Redlands diversion), GR1 (Green River from Colorado River to just downstream of Desolation-Gray Canyon), GR2 (Green River, Desolation-Gray Canyon) and GR3 (Green River from upstream end of Desolation-Gray Canyon to mouth of Whirlpool Canyon). We recognize, however, the potential for confounding by including river reach as a covariate. The two rearing facilities, GVEFF and ONFH, each stocked distinct river reaches with the exception of GR1, where they overlapped. Thus, the groups (rearing methods) specific to each facility will be confounded with river reach and care must be taken to limit comparisons among groups and within reaches accordingly.

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

Some covariates may act as surrogates for other variables affecting razorback sucker survival and/or capture probability. Stocking year could supply information relating to any annual variation (environmental conditions, hatchery circumstances, or sampling variation). Year was evaluated using time model structures (see "*A priori model set*" below). Stocking season is another covariate which provides information about environmental conditions that may vary seasonally, 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, we determined that stocking season as defined was a suitable surrogate for other seasonally varying, but potentially confounded, 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 batch of stocked razorback suckers and all other stocking information (year class, lot number, date) was identical among records for that batch, we calculated the mean of reported lengths and assigned it to remaining records for that batch. Those individuals with no reported TL and not part of a batch from which mean TL could be obtained were eliminated from analysis. The importance of the fish TL effect on razorback sucker survival (Zelasko et al. 2009) was determined an acceptable tradeoff for the exclusion of the relatively few records (0.01%) without length information. Razorback suckers that were assigned mean batch lengths and those which were eliminated from analysis were presumed to be representative of the entire dataset.

Since 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, we did not include weight as a covariate. Moreover, only 8.7% of all records of razorback suckers stocked from 2004–2007 contained fish weight data. If more records

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

Encounter histories

We constructed razorback sucker encounter histories by building a Microsoft Access query that returned stocking year and subsequent recapture years for every stocked fish in the hatchery release portion of the database. Capture occasions occurred annually and the time interval between capture occasions for this study was defined as 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 times of stocking and sampling caused the actual length of time intervals between capture occasions to vary among years. Fish stocked during spring, summer, or autumn (96.2%) would have been at large at least six months, since most sampling in the basin does not commence until mid-spring of the following year. However, regardless of the time at large for newly stocked razorback suckers, captures of individuals that occurred in consecutive calendar years were considered two occasions, even though fish may have been at large less than 12 months.

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

In addition to the encounter history, input data lines included the encounter history's frequency in the group (rearing method) to which it belonged, followed by all individual covariate values. The frequency of an individual encounter history was always "1" by definition, except when a fish has died upon recapture, when its frequency was "−1." Individual covariates were entered as continuous, numerical values (such as TL) or as “dummy” variables, placeholders that represent specific categorical covariates (such as river reaches of stocking) populated with 0s and 1s.

Statistical modeling

Data were analyzed in Program MARK (White and Burnham 1999) using the Cormack-Jolly-Seber (CJS) open population model (Cormack 1964; Jolly 1965; Seber 1965) and other closely related models. Model assumptions include: tagged individuals are representative of the population to which inference is made, numbers of releases are known, tagging does not affect survival, no tags are lost and all tags are 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 recapture 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 were apparent survival and recapture 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. Recapture probability, p_j, is the conditional probability of recapture in year j, given the individual is alive at the beginning of year j. The number of individuals released in year i, R_i, is known and includes releases of newly tagged individuals, plus releases of recaptured individuals. The random variable, m_{ij}, is the number of recaptures in year j from releases in year i (Table 1).

A priori model set

After preparing the final dataset for input, we used the previously identified groups and covariates to build an a priori model set. Additional effects were modeled directly within MARK. Survival rate, φ, model structures included the following effects:

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

group (*g*) - survival rate estimates vary by method employed to rear fish (tank, pond, intensive);

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

first 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); may lack predator avoidance, current conditioning, or other survival skills;

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 changing with increasing total length;

season (season) - 1st-interval survival rates vary by season when fish were stocked (spring, summer, autumn, winter);

river reach (reach) - 1st-interval and subsequent-interval survival rates vary by river reach into which fish were stocked (CO2, CO3, GU2, GR1, GR3);

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

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

group (*g*) - recapture probability estimates vary by method employed to rear fish (tank, pond, intensive);

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

first river year (ry1) - 1st-occasion recapture probabilities are different from subsequent-occasion probabilities (i.e., for a given capture occasion [year], fish have a different recapture probability if it is their first capture occasion in the river after stocking than if it is a subsequent occasion); may be more or less active in a new environment due to displacement or disorientation, resulting in higher or lower recapture probabilities;

river reach (reach) - 1st-occasion and subsequent-occasion recapture probabilities vary by river reach into which fish were stocked (CO2, CO3, GU2, GR1, GR3); e.g., *p* of GR1 is not the probability of recapturing fish in GR1, but, instead, of recapturing fish stocked into GR1 but recaptured in any reach;

total length at stocking (TL, TL^2) - 1st-occasion recapture probabilities are related to total length at time of stocking.

Run procedure and model selection

For each parameter, effects were modeled individually, additively, and as interactions. Due to the large dataset and numerous a priori model structures for each of the φ and *p* parameters (n = 80 and 51, respectively; Appendix A), running every combination of model structures and relying on model averaging would have required an inordinate amount of computation time. Therefore, a more efficient procedure to run candidate models was employed. A complex additive model, which contained many of the hypothesized influential effects, was chosen. For initial runs, the complex structure for the φ portion of the model remained the same, while the *p* portion was simplified. The aim of this strategy was to force the more complex φ structure to absorb much of the variance, allowing better estimation of *p*. Complexity of *p* structure was gradually increased, using parameter estimates from each previous model as starting values to aid in estimation. Once all a priori model structures for *p* had been run with the complex φ structure, the *p* structure from the best model was retained and run with all variations of φ, starting with the simplest structure. We ran all models using the logit link to maintain a monotonic relationship with the continuous individual covariate, TL. Model selection was conducted with Akaike's information criterion (AIC, Akaike 1973). Models with lower AIC values are considered more parsimonious and closer to the unknown "truth" that produced the data (Burnham and Anderson 2002). The AIC values reported by Program MARK are based on a modified version of the criterion, denoted AIC_c, which adjusts for small sample size bias (Sugiura 1978; Hurvich and Tsai 1989; Burnham and Anderson 2002) and converges with AIC when sample size is large.

RESULTS

Data summary

The final dataset for parameter estimation consisted of 96,448 records of razorback suckers stocked from 2004–2007 and 1,511 recapture events of 1,470 unique individuals from 2005–2008. Most stocked fish in this study were reared using the intensive method (46.4%), followed by pond (33.4%) and tank (20.2%) methods. All methods were represented each year, except in 2004 when no tank fish were stocked. Stocking occurred in the UCRB every year from 2004 through 2007 and ranged from 17,432 in 2005 to 30,935 in 2006. Stocking occurred in each year during autumn (57% of total) and summer (37%), but was less consistent in winter (4%) and spring (2%). Fish reared by each method were stocked during both autumn and summer, but no tank fish were stocked in winter and only five tank fish were stocked during spring (Table 2). Razorback suckers were stocked each year of the study into reaches CO2 (33% of all fish stocked), GR3 (26%), and GR1 (25%). Fish were only stocked into reach GR2 in 2006 (10% of all fish stocked) and GU2 in 2006 and 2007 (6%). As expected, rearing methods were closely associated with specific stocking reaches (Table 3): reaches CO2 and GU2 were only stocked with tank- and pond-reared razorback suckers, while reaches GR3 and

GR2 were only stocked with intensively-reared fish. Reach GR1 received fish reared by all three methods.

Fish lengths at stocking ranged from 117–560 mm TL with a mean of 301.5 mm TL (Figure 4). Pond-reared razorback suckers were stocked at the largest mean TL (309 mm), followed by intensive (298 mm TL) and tank (296 mm TL). There was no more than a 3-mm difference in mean TL of fish stocked during 2004, 2005, and 2007 (range: 304–307 mm), but those stocked in 2006 averaged 293 mm TL (Table 4). Mean lengths of stocked fish per season ranged from 293 mm TL in winter to 320 mm TL in spring (Table 2). Reach CO2 received the largest stocked fish (306 mm TL) and reach GR2 the smallest (290 mm TL), on average (Table 3).

Recaptures of stocked razorback suckers occurred on every capture occasion. Most recapture events were in 2008 (43%), followed by 2006, 2005, and 2007, in descending order (Table 5). The largest portion of recaptures consisted of individuals stocked in 2004 (43%), then 2005, 2007, and 2006, in descending order. Most recaptures were of pond-reared razorback suckers (68% of individuals), followed by intensive (31%) and tank (1%). Fish stocked in autumn made up more than 86% of recaptured individuals (Table 6). Razorback suckers stocked into reach GR1 produced the most recaptures (40%), followed closely by reach CO2 (36%, Table 7). Lengths at stocking for razorback suckers that were subsequently recaptured ranged from 172–515 mm TL with mean of 332 mm TL (Figure 4).

A priori model set

A complete list of φ and *p* model structures considered for analysis can be found in Appendix A.

Model selection

Relatively parameter-rich models that included interactions of group and time effects produced many inestimable parameters and were removed from consideration, resulting in a reduced set of reasonable models. There were more than 50 models in the resulting set (Appendix B), 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 81% of AIC_c weight, and the next closest models were within about 5 AIC_c points of the top-ranked model (Table 8). The difference between the top- and second-ranked models was the absence of the rearing method effect in the lower-ranking model's recapture probability structure. Since the effect of acclimation was of primary interest in this study, we did not investigate results of the second-ranked model. The difference between the top- and third-ranked models was the structure of the stocking reach effect in the survival portion of the models: in the top-ranked model, stocking reach was configured to affect only the first survival intervals of razorback suckers; while, in the third-ranked model, stocking reach continued to affect all survival intervals. Given that we previously found substantial movement of razorback suckers out of their stocking reaches (Zelasko et al. 2009), much of which occurred during first intervals in the river, we did not investigate results of the third-ranked model any further. Therefore, the top-ranked model was chosen for further inference. Goodness of fit testing was not possible due to sparse data and inclusion of individual covariates.

Parameter estimates

Survival.—The top-ranked model produced 29 estimable parameters. Survival was modeled with 16 parameters: an intercept, two group parameters, three intervals, 1st-interval effect, three stocking season effects, four stocking reach effects, and both linear and quadratic effects of TL (Table 9). The intercept represented the third group through the fourth interval.

The 1st-interval effect also acted as an intercept for covariates, representing 1st-interval survival of fish stocked during the fourth season into the fifth reach. Overall, slightly larger positive logit values for tank- and pond-reared razorback suckers suggested higher survival than the intensively-reared group. However, overlapping 95% confidence intervals (CIs) indicated no statistical difference at that level. Large negative logit values signified lower survival for fish through their first intervals in the river (ry1). This was particularly true if razorback suckers were stocked during summer or into reach CO2 or GU2. The model ultimately produced 249 survival rate estimates for stocked razorback suckers: four time-varying, TL-dependent, 1st-interval φ's for fish reared by each of three methods, then stocked during each of four seasons and into each of five reaches; plus three time-varying, subsequent-interval φ's for fish reared by each of three methods.

1st-interval survival.—First-interval survival rates, ry1 φ's, were low: mean rate for average-sized razorback suckers (301.5 mm TL) reared by any method was 0.09, when averaging across stocking year, season, and reach for each method. Survival rates through first intervals were highest for intensively-reared razorback suckers (mean = 0.13), followed by pond-reared (0.09) and tank-reared (0.03) fish (Figure 5). Pond- and intensively-reared fish of average length stocked in 2004 had predicted ry1 φ's approximately 3–5 times higher than in other years of stocking. No tank-reared fish were stocked that year.

Total length at stocking had a large and positive effect on 1st-interval survival rates of razorback suckers stocked in the Upper Colorado River Basin (Figure 6). Averaging over seasons and reaches of stocking for each rearing method, predicted ry1 φ's of razorback suckers stocked at less than 200 mm TL were low for all years and methods (range: 0.002–0.027) but increased to 0.67–0.97 for the few fish >500 mm TL. First-interval survival rates for razorback suckers stocked at the average length of 301.5 mm TL were also low: ranging from 0.02–0.08 for fish reared by all three methods and stocked from 2005–2007, but increasing to 0.20–0.26 for pond- and intensively-reared fish stocked in 2004. Increasing TL at stocking from

300 to 400 mm yielded predicted ry1 φ's 3–3.5 times higher for razorback suckers stocked in 2004, and 6–10 times higher for those stocked from 2005–2007, depending on rearing method. For each rearing method, ry1 φ estimates averaged over stocking season and reach were lower than the subsequent-interval estimates (see below) for razorback suckers of most sizes at stocking, but increased as length at stocking increased. For intensively-reared fish, ry1 φ estimates did not exceed that method's mean subsequent-interval survival estimate until size at stocking reached 480 mm TL. That overlap was not achieved for pond- and tank-reared fish until sizes at stocking reached 550 and 600 mm TL, respectively.

Season of stocking also had a large effect on 1st-interval survival rates of stocked razorback suckers. For each rearing method and survival interval (averaging across stocking reaches), predicted ry1 φ of a 301.5-mm-TL fish was highest when stocked in spring, followed by autumn, winter, and summer, in descending order (Figure 7). Intensively-reared razorback suckers had similar estimate ranges for fish stocked from 2005–2007: 0.18–0.23 for spring-stocked fish down to 0.02–0.03 for summer-stocked fish. Estimates for those stocked in 2004 were 2–5 times higher (range: 0.10–0.54), depending on season of stocking. Pond-reared razorback suckers stocked from 2005–2007 had predicted seasonal survival rate estimates ranging from 0.11–0.15 (spring) to 0.01–0.02 (summer), while those stocked in 2004 had rates ranging from 0.06–0.40. Seasonal effect estimates for tank-reared razorback suckers stocked in seasons other than summer were unreliable, since 94% of that group was stocked during summer and those stocked during other seasons were not recaptured.

Logit values and overlapping CIs for river reaches of stocking indicate similar effects when razorback suckers were stocked into reaches CO2 or GU2, as well as when stocked into any of the GR reaches (GR1 was represented by the covariate intercept, ry1; Table 9). Only tank- and pond-reared fish were stocked into reaches CO2 and GU2. First-interval survival rate estimates for 301.5-mm-TL razorback suckers stocked into those reaches (averaging across each method's seasons of stocking) were low, not exceeding 0.03 in most intervals and only reaching 0.12 for fish stocked in 2004 (Figure 8). Only intensively-reared fish were stocked into reaches GR3 and GR2, where ry1 φ estimates ranged from 0.05–0.08 for most intervals but were as high as 0.26 for razorback suckers stocked in 2004 (Figure 8). Reach GR1 received stocked fish reared by all three methods. Pond-reared fish had predicted ry1 φ's ranging from 0.27–0.66 when stocked into GR1, averaging across seasons of stocking. Intensively-reared fish were predicted to survive at only slightly higher rates when stocked in GR1 (0.09–0.36, depending on the interval) than GR2 or GR3. Survival estimates for tank-reared razorback suckers stocked into reach GR1 were higher than for other reaches: 10 of the 12 recaptures for that group were fish stocked into GR1. However, estimates had very wide 95% CIs owing to few recaptures of that group overall.

Subsequent-interval survival.—Predicted survival rates for stocked razorback suckers after their first intervals in the river varied by rearing method and time, but were all high. Mean rates for tank-, pond-, and intensively-reared individuals were 0.94, 0.92, and 0.79, respectively (Figure 9). Rates for all rearing methods were slightly lower for the 2006–2007 interval, but the differences among all rearing methods and intervals were not significant based on broadly overlapping 95% CIs. Estimates for tank-reared fish had exceptionally wide CIs and were calculated with only four subsequent-interval recaptures.

Recapture probability.—In the 29-parameter, top-ranked model, recapture probability was modeled with 13 parameters: an intercept, two group parameters, three occasions, 1st-occasion effect, four stocking reach effects, and both linear and quadratic effects of TL (Table 10). The intercept represented the third group on the fourth occasion. The 1st-occasion effect also acted as an intercept for covariates, representing 1st-occasion recapture probability of fish stocked into the fifth reach. A large negative logit value for tank-reared razorback suckers indicated lower recapture probability for fish reared by that method. A positive logit value indicated somewhat higher recapture probabilities for fish on their first capture occasion in the river after stocking, particularly if they were stocked into reach CO2 or GU2. The model produced 69 recapture probability estimates for stocked razorback suckers: four time-varying, TL-dependent 1st-occasion *p*'s for fish reared by each of three methods and stocked into each of five reaches, plus three time-varying, subsequent-occasion *p*'s for fish reared by each of three methods.

1st-occasion recapture probability.—First-occasion recapture probabilities, ry1 *p*'s, for razorback suckers of mean length at stocking (301.5 mm TL) were higher when fish were pond-reared (0.12–0.31) than intensively-reared (0.03–0.09) or tank-reared (0.01–0.02), when averaging across each group's stocking reaches (Figure 10). Probabilities varied by occasion and were highest in 2008 for all groups. Because no tank-reared fish were stocked in 2004, there were no ry1 *p*'s calculated for that group in 2005.

Logit values for both TL and TL^2 effects overlapped zero, indicating no statistical significance. The resulting effect was slightly positive for razorback suckers stocked at lengths up to 180 mm, but decreased for larger fish. The relationship was unexpected, given that razorback suckers stocked at larger sizes were generally recaptured in higher proportions than those at which they were stocked (Figure 4).

Tank- and pond-reared razorback suckers stocked into reaches CO2 and GU2 had higher ry1 *p*'s than those stocked into GR1, and tank-reared fish stocked into any of those reaches had lower probabilities than pond-reared fish. Predicted 1st-occasion recapture probabilities of 301.5-mm-TL tank-reared razorback suckers ranged from 0.01–0.03 when stocked into reaches CO2 and GU2, but only 0.004–0.009 when stocked into reach GR1 (Figure 11). First-occasion recapture probabilities for the same length pond-reared razorback suckers ranged from 0.16–0.39 when stocked into reaches CO2 and GU2, but only 0.04–0.13 when stocked into GR1. Intensively-reared razorback suckers were stocked into reaches GR3, GR2, and GR1, but most often into GR3. First-occasion recapture probabilities for 301.5-mm-TL individuals stocked into reach GR3 ranged from 0.02–0.08, and were nearly the same for those stocked into GR1 (Figure 12). Intensively-reared razorback suckers were only stocked into reach GR2 in 2006, and their ry1 *p* in 2007 was higher than for those stocked into other reaches: 0.07.

Subsequent-occasion recapture probability.—Predicted recapture probabilities for stocked razorback suckers after their first occasions in the river varied by rearing method and occasion, and were all 0.05 or lower (Figure 13). Mean subsequent-occasion recapture probabilities for pond-, and intensively-, and tank-reared fish were 0.04, 0.02, and 0.002, respectively. Probabilities were highest in 2008 for all rearing methods.

DISCUSSION

Evaluation of stocking programs designed to enhance populations of depleted fishes is an essential part of a well-informed adaptive management process. Our analysis of razorback sucker tag-recapture data collected since implementation of an integrated stocking plan for the UCRB showed low 1st-year survival for fish reared by any method, but highest for intensively-reared individuals. Further, survival was positively related to fish length at stocking, but only modest for fish of average length, and was particularly low in summer. Stocking reach was too intertwined with rearing method to yield useful results. Survival of stocked fish after their first intervals in the river was higher. Recapture probabilities were low, but slightly higher for first capture occasions after stocking. Below we discuss these findings in more detail and recommend changes in stocking protocols that may improve survival of stocked fish and increase prospects for recovery of razorback suckers.

Apparent survival, φ, vs. true survival, S, and Bias

Apparent survival differs from true survival in that apparent survival is the probability of an individual surviving an interval, given that it was alive at the start of the interval and in the study area available for capture. Thus, $1 - \varphi$ 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 Cataract Canyon upstream of upper Lake Powell, downstream of its confluence with the Green River. It is not known, however, if razorback suckers stocked into the UCRB are displaced downstream into Lake Powell.

Although PIT tag loss was assumed to be low for this study, especially compared to the dorsally-attached Carlin tags used from 1980–1992 (Prentice et al. 1990; McAllister et al. 1992; Ombredane et al. 1998; Ward and David 2006), faulty scanning equipment, lack of scanning, and data recording errors may cause virtual tag loss and potentially biased estimates of survival (Bestgen et al. 2002). Because recapture rates are already relatively low, accurate tagging, tag detection, and data recording are minimal requirements to understand provenance of captured fish and recruitment rates of razorback suckers.

1st-interval survival

Survival rates of stocked razorback suckers through their first intervals in the river were lower than those through subsequent intervals, regardless of rearing method or reach, season, and length at stocking. This result is not particularly surprising, given the relatively benign hatchery environment in which many fish are raised for 1.5 – 2.5 years prior to stocking: stable or no flow velocity, constant temperatures, dependable and abundant food, and predator-free habitats may leave fish unprepared for conditions encountered upon release (Suboski and Templeton 1989; Olla et al. 1998). The gravel pit ponds, occupied by nonnative species and not supplemented, are exceptions. Excessive post-release mortality has been a problem faced by hatcheries for decades (Miller 1954; Flick and Webster 1964; Pitman and Gutreuter 1993; Stahl et al. 1996), and such mortality continues to plague recent conservation efforts to reestablish declining species in their native ranges (Brown and Day 2002). For example, white sturgeon

(*Acipenser transmontanus* Richardson) stocked into the Kootenai River, Idaho, exhibit first-year survival rates 30% lower than in subsequent years (Ireland et al. 2002; Justice et al. 2009). 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. 2008).

Hatchery-reared razorback suckers have also demonstrated poor post-stocking survival in several other studies. It has been estimated that 900 razorback suckers/km of river could be consumed by ictalurid catfish within 24 h of being stocked in the Gila River, Arizona, which likely resulted in nearly 100% mortality (Marsh and Brooks 1989). Marsh et al. (2005) estimated first-year survivorship to be ≤ 0.26 for most razorback suckers stocked in Lake Mohave from 1999–2002. A capture-recapture study of stocked razorback suckers in the lower Colorado River from 2006 to 2008 estimated overall annual survivorship to range from near zero for 300 mm TL fish to 0.28 for fish 400 mm or larger (Schooley et al. 2008). We estimated that razorback suckers of average length (252.5 mm TL) stocked into the UCRB from 1995–2005 survived at a rate of 0.05, when averaging across stocking season (Zelasko et al. 2009). Increasing TL at stocking to 300 mm resulted in a predicted survival rate estimate of 0.15, slightly higher than the 0.09 predicted for razorback suckers of similar size stocked during the more recent 2004–2007 study period.

This study investigated how rearing method, season, year, and reach of stocking, and total length at stocking affected 1st-year survival of razorback suckers. Disproportionate numbers of tank-reared fish stocked across seasons combined with relatively few recaptures (<0.1%) produced spurious, imprecise results for that rearing method. We ran the top models from this analysis with a data set excluding tank-reared razorback suckers and all estimates were markedly similar. Thus, in order to be comprehensive, we retained the tank-reared group in our analysis.

Tank-reared razorback suckers had a higher logit value for survival than pond- or intensively-reared fish but an exceptionally wide 95% CI that overlapped zero, indicating no statistically significant difference from the intercept (intensively-reared fish). Most importantly, tank-reared fish produced the lowest estimates of 1st-interval survival when averaging across each method's stocking seasons and reaches. Nearly all of those fish (94%) were stocked during summer, the stocking season which produced the lowest survival rate estimates. Given the confounding of rearing method with stocking season, we cannot attribute the low 1st-interval survival of tank-reared fish to one variable. However, stocking during summer produced similarly low mean survival rate estimates for pond- and intensively-reared razorback suckers (0.03–0.04) as for tank-reared (0.03). Furthermore, summer-stocked fish were recaptured in the lowest proportion overall (0.25%) and for pond-reared fish, specifically (0.53%), compared to other seasons (Table 11). Only 0.07% of tank-reared fish stocked during summer were recaptured (n = 12), while none of the few fish stocked during spring or autumn were ever seen again during the study period. Although only 0.39% of intensively-reared, summer-stocked razorback suckers were recaptured, winter-stocked fish recaptures were even lower for that method (0.12%).

Our previous survival rate analysis for razorback suckers stocked from 1995–2005 (Zelasko et al. 2009) also found that stocking during summer produced the lowest survival rate estimates. While that analysis produced tightly grouped estimates for all other stocking seasons, we calculated decreasing mean survival rates in this study for fish stocked during spring (0.20–0.29, depending on rearing method), autumn (0.12–0.18), and winter (0.05–0.08), respectively. A similar analysis for razorback suckers stocked into the San Juan River Basin, 1994–2007, found lowest survival rate estimates for winter-stocked fish in a year of average hydrologic conditions (0.02%, Bestgen et al. 2009).

Pond- and intensively-reared razorback suckers stocked in 2004 survived their first intervals in the river at higher rates than fish stocked in other years. No tank-reared fish were stocked and the smallest proportion of all summer-stocked fish (11%) was released that year. Razorback suckers released in 2004 produced the highest percent of recaptures (1st- and subsequent-interval recaptures combined) per stocking year (3%) and of all recaptures (43%, Table 12). Furthermore, a higher percent of the 2004 cohort was recaptured on their first capture occasion (i.e., 2005, 1.35%) than those stocked in 2005 (1.14%), 2006 (0.37%), or 2007 (1.12%).

Effects of stocking reach on 1st-interval survival rates were inextricably confounded with rearing method, since only tank- and pond-reared razorback suckers were stocked into reaches CO2 and GU2 and only intensively-reared fish were stocked into reaches GR3 and GR2. No substantial within-method differences in survival were found for fish stocked into the above reaches. Reach GR1 was stocked with razorback suckers reared by all three methods. Tank-reared fish stocked into GR1 survived at higher rates than when stocked elsewhere, but the differences were not significant, based on an exceedingly wide 95% CI for that reach. Pond-reared fish, however, survived at markedly (and significantly) higher rates when stocked into GR1. Notably, 100% of tank-reared razorback suckers stocked into GR1 were released during summer, whereas 90% of pond-reared fish stocked into that reach were released during autumn. There were no noticeable differences among intensively-reared fish stocked into any of the GR reaches. Comparisons of survival among razorback suckers reared by each method and stocked into reach GR1 are not possible due to very little overlap of releases by year and season (Table 13). The effect of stocking reach was not retained in the top models to estimate survival of razorback suckers stocked from 1995–2005, which may have been the result of movement out of stocking reaches over so many years (i.e., fish may not have been “surviving” in the reaches into which they were stocked). That study recommended further investigation of the effects of stocking reach since implementation of the integrated stocking plan, but the differences found among reaches in this study cannot be separated from the effect of rearing method or season of stocking.

Increasing total length at stocking resulted in increased 1st-interval survival rate estimates for all rearing methods. The same pattern was observed for razorback suckers stocked in the UCRB from 1995–2005 and in the San Juan Basin from 1994–2007 (Bestgen et al. 2009; Zelasko et al. 2009). For all intervals in this study, TL-dependent survival rate curves were steeper than the average curve estimated for fish stocked from 1995–2005 into the UCRB (Figure 14). However, survival rate estimates in this study did not surpass those in the previous analysis until sizes at stocking reached 410–510 mm TL, depending on rearing method. Beyond those length thresholds, fish stocked at similar sizes were predicted to survive at higher rates when stocked from 2004–2007 than 1995–2005. Incidentally, recommended size-at-stocking of razorback suckers repatriated into Lake Mohave is 500 mm – a size believed to increase survival, limit predation by nonnative species, and accelerate development of brood stock (Lower Colorado River Multi-Species Conservation Program 2006).

Several studies have investigated other possible underlying causes of high post-stocking mortality in razorback suckers, such as lack of acclimation, conditioning, and predator avoidance. Site acclimation to reduce downstream displacement of stocked razorback suckers has long been recognized as a need, but not widely implemented (Mueller and Foster 1999; Mueller et al. 2003; Kegerries and Albrecht 2009). Recent investigations of Colorado pikeminnow stocked into the San Juan River demonstrate that acclimation may increase retention (Golden et al. 2006). Exercise conditioning was found to increase swim performances of razorback suckers by 26% (Ward and Hilwig 2004) and may reduce downstream displacement to unsuitable habitats. Combined predator exposure and exercise conditioning showed promising results for razorback sucker survival: treatment fish (exercised and exposed to predation) experienced significantly lower mortality 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 higher mortality rate for control fish was conservative compared to a truly naïve group, unable to learn from more predator-savvy conspecifics. Similarly, exposure to predators and chemical cues of predators successfully induced anti-predator behavior in other species (Brown and Smith 1998; Olla et al. 1998; Arai et al. 2007) and may be useful to develop anti-predator behavior in razorback suckers.   Predator-avoidance training and exercise conditioning of hatchery-reared razorback suckers may increase low 1st-interval survival.

Subsequent-interval survival

Mean survival rate estimates for razorback suckers reared by any method through all intervals subsequent to their first interval in the river ranged from 0.79 to 0.94 and were all higher than the assumed adult survival rate in the integrated stocking plan (0.70, Nesler et al. 2003) and the subsequent-interval rate estimated in our previous analysis (0.75). They also exceeded the survival rates estimated for wild adult razorbacks in the middle Green River (0.71–0.76) from 1980 – 1999 (Modde et al. 1996; Bestgen et al. 2002). Intensively-reared razorback suckers had lower subsequent-interval survival rate estimates than fish reared by other methods. However, 95% CIs for all methods overlapped, and those for tank-reared fish were particularly wide. Indeed, only 12 tank-reared razorback suckers were ever recaptured (eight only on the first capture occasions after being stocked and four on subsequent occasions), resulting in very little data to estimate subsequent-interval survival of that group.

High subsequent-interval survival rates for fish reared by all methods, observations of stocked razorback suckers in spawning aggregations with wild individuals (Modde et al. 2005), and annual production of larvae in the Green River since 2000, presumably from stocked fish (K. Bestgen, unpublished data), suggest that hatchery-reared fish are capable of acclimating to the riverine environment and may contribute to recovery if recruitment bottlenecks can be overcome.

Stocking goals

The current razorback sucker stocking plan for the UCRB (Nesler et al. 2003) requires the release 9,930 age-2 (300 mm TL) fish for six consecutive years to reach the goal of 7,540 adults in each population (5,800 adults plus 30% buffer). The protocol assumes survival rates of 0.50, 0.60, and 0.70 for age-2, age-3 (350 mm TL), and age-4 (400 mm TL) fish, respectively. However, our analysis resulted in 1st-interval survival rate estimates considerably lower than those assumed rates.

By replacing assumed rates with mean ry1 (TL-dependent) and mean post-ry1 survival rate estimates generated in this study, we found that 300 mm TL razorback suckers could be stocked at the current level indefinitely without ever attaining the adult population goal. In order to meet the goal in the six-year period originally stipulated by the plan, 42,900 age-2 (300 mm TL) razorback suckers would have to be stocked annually for each population of 7,540 adults (Table 14). Allowing ten years to achieve the goal with the same size fish would require annual stocking of 28,100 individuals. Increasing length at stocking to 400 mm TL but releasing the same numbers of razorback suckers specified in the current plan would technically reach the adult population goal in the first year of stocking (400 mm TL razorback suckers are considered age-4 adults in the integrated plan). If the current level of stocking those larger fish continued for six years, each population could number nearly 25,000 adults (Table 15). Ten years could generate 30,000 adults per population. All estimates assumed low or no survival of larval and juvenile life stages and, therefore, no recruitment that would supplement stocked fish.

Our calculations used mean survival rate estimates, averaging across rearing methods (excluding tank) and seasons and reaches of stocking. Group-specific results could be used to further refine propagation and stocking protocols. We recognize, however, that rearing facilities operate under certain physical and financial constraints. Therefore, a cost-benefit analysis of raising razorback suckers to larger sizes and refraining from releases during some seasons must be performed to realistically determine the best approach to improving survival.

Recapture probability

Recapture rate of hatchery-reared razorback suckers was low: 1,470 (1.5%) of 96,448 individuals. That is only slightly higher than the 1.1% recapture rate observed in our analysis of razorback suckers stocked from 1995–2005. Accordingly, recapture probability estimates were all low: mean 1st-occasion and subsequent-occasion estimates were 0.10 and 0.02, respectively.

Recapture probability is linked to survival estimation as follows:

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

which states that the log-likelihood of the parameters, given the encounter histories (EH) observed, is equal to the summation of the product of the number of animals that share an encounter history and the log of the probability of that encounter history. The probability of an encounter history is the product of an animal's survival rates and recapture probabilities (or 1 – recapture probabilities, if not recaptured) for all intervals and occasions. Increasing recapture probabilities results in more precise survival estimates (Lebreton et al. 1992), so it is worthwhile to design studies with that in mind. In this study, we found that rearing method, time since stocking, size of stocked fish, reach of stocking, and capture year all may have affected recapture probabilities.

1st-occasion and subsequent-occasion recapture probabilities

Both 1st- and subsequent-occasion recapture probabilities were lowest for tank-reared razorback suckers. This was expected, given that only 12 fish reared by that method were ever recaptured. Pond-reared fish made up 68% of recaptures and produced the highest recapture probability estimates. Intensively-reared razorback suckers had intermediate estimates.

Both 1st- and subsequent-occasion recapture probability estimates were highest in 2008. More sampling effort occurred in the UCRB during that year than any other: Colorado pikeminnow abundance estimate sampling and non-native fish removal sampling were conducted in both the Colorado and Green River subbasins, and humpback chub abundance estimate sampling also occurred in the Colorado River subbasin that year. In contrast, sampling during 2005 (the year with lowest predicted recapture probabilities) consisted only of Colorado pikeminnow and humpback chub abundance estimate sampling in the Colorado River subbasin and non-native fish removal sampling in the Green River subbasin. Sampling efforts in 2006 and 2007 included non-native fish removal sampling in both subbasins, and both Colorado pikeminnow and humpback chub abundance estimate sampling in the Green River subbasin. Humpback chub sampling also occurred in the Colorado River subbasin during 2007.

Since nearly all razorback sucker recaptures resulted from the aforementioned sampling efforts, one might expect time-varying recapture probabilities to parallel those estimated for Colorado pikeminnow in abundance estimate analyses. However, estimated capture probabilities for Colorado pikeminnow in the Green River subbasin were lower in 2008 than 2006 or 2007 (Bestgen et al. 2010). Low estimates that year were attributed to relatively high and cool flows (Figure 15), which may have reduced sampling efficiency and availability of fish for capture. A more detailed investigation into the dates and projects under which razorback suckers were recaptured in 2008 would be necessary to understand the inconsistency between the species' recapture probability estimates.

The 1st-occasion (ry1) effect on recapture probabilities was slightly positive, but not different from the model's intercept, based on the logit value's 95% CI. Comparable results were found in our previous analysis, where recapture probability estimates for razorback suckers' first sampling occasions after stocking were barely higher than estimates for subsequent occasions. However, models with the effect ranked higher than those without it in both studies. It may be that the ry1 effect was merely acting as the intercept for covariates in both model structures. Thus, the small effect was retained in the top models despite its lack of statistical significance.

Conversely, it is unknown why both statistically insignificant TL and TL^2 effects were retained in the recapture probability portion of the top model. Removing the effects resulted in a model ranked fifth and approximately 42 AIC_c units away from the top model (Table 8). The relationship produced by the TL and TL^2 effects predicted highest recapture probabilities for fish stocked at 180 mm TL and decreasing estimates for larger fish, which conflicted with the fact that the mean size at stocking for recaptured fish was 332 mm TL (Figure 4).

The top model in the previous analysis of razorback suckers stocked from 1995 through 2005 also contained logit values for TL and TL^2 that were not different from the model's intercept (Zelasko et al. 2009). However, the 95% CIs for the effects did not overlap zero as broadly as in this analysis. Regardless, we chose to retain the effects in the previous analysis, because length generally affects recapture probability of fishes (Anderson 1995; Bestgen et al. 2007a; Dauwalter and Fisher 2007; Korman et al. 2009) and we wished to demonstrate ways to increase that probability. The resulting relationship predicted increasing recapture probabilities for fish stocked at lengths up to 390 mm and decreasing for larger fish, which was concordant with actual recapture data (Zelasko 2008).

We suggest that the unexpected relationship between TL and recapture probability generated by this analysis may have been due to the increased size uniformity of stocked razorback suckers in recent years. In our previous analysis, 50% of stocked fish measured between 250 and 350 mm TL, and remaining fish were spread more widely among length categories. As recommendations for size at stocking were implemented, 83% of fish stocked from 2004 to 2007 fell between 250 and 350 mm TL. Perhaps the data set did not contain enough variation to develop a strong relationship between length at stocking and recapture probability.

While reaches of stocking did not appreciably affect recapture probabilities of intensively-reared razorback suckers, tank- and pond-reared fish had lower 1st-occasion recapture probabilities when stocked into reach GR1 than when stocked into CO2 or GU2. This may not be intuitive, as fish of each rearing method stocked into reach GR1 were recaptured in higher proportions than those stocked into other reaches (Table 16) and pond-reared fish stocked into that reach produced the highest survival rate estimates. However, the high recapture proportion of fish with low recapture probabilities can produce relatively high survival rate estimates for those fish.

Subsequent-occasion capture probability estimates were all 0.05 or lower and there were no statistically significant differences among capture occasions (years) within any rearing method. Estimates for tank-reared razorback suckers were particularly imprecise, as only four were ever recaptured after their first post-stocking capture occasions.

Ultimately, increasing capture probability must become a priority if more precise parameter estimation is desired. 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 recapture probability. Although this study improved on that aim compared to the previous analysis, data were still collected from a variety of sampling programs where effort was sometimes low after stocking substantial numbers of fish, and very few efforts specifically targeted stocked razorback suckers. In contrast, species-specific, Colorado pikeminnow abundance estimate sampling produced recapture probabilities ranging from 0.01 to 0.20 in the Green River subbasin, 2000–2003 (Bestgen et al. 2007a) and 0.07 to 0.19 in the Colorado River subbasin, 1991–1994 (Osmundson and Burnham 1998). Future recapture probability estimations would be aided by more consistent sampling efforts targeted specifically at razorback suckers, particularly in years when other intensive sampling, for studies such as Colorado pikeminnow abundance estimation, is not occurring. Not only would recapture probabilities likely increase, but a uniform protocol would better meet the underlying assumption that recaptures are made within brief time periods relative to intervals between tagging. Additionally, remote PIT tag stations placed near known spawning areas would provide valuable encounter data with little effort. Recapture rates of razorback suckers stocked in the lower

Colorado River, 2006–2008, were 9% or less with electrofishing and trammel netting, but increased to 39% when remote PIT-tag scanning was employed (Schooley et al. 2008). A capture-recapture study on Lost River suckers in Oregon estimated low recapture probabilities (0.02–0.15) when using only physical recaptures, but 0.91 or higher after employing a remote detection system (Hewitt et al. 2010). Furthermore, the increased encounters improved precision of parameter estimates to such a degree that CIs became negligible.

CONCLUSIONS

The imbalance in numbers of razorback suckers reared by three methods and stocked across seasons, years, and reaches limited our ability to estimate the effects of some of those variables on survival of stocked fish. However, we were able to demonstrate once again that 1st-interval survival of razorback suckers was dramatically lower than subsequent-interval survival. As in our previous analysis of fish stocked from 1995 through 2005, 1st-interval survival was lowest for those stocked during summer and was positively related to size at stocking. Tank-reared fish exhibited the lowest 1st-interval survival (but nearly all were stocked during summer), followed by pond-reared and intensively-reared, in ascending order. Razorback suckers stocked during 2004, when no tank-reared and the fewest summer-stocked fish were released, produced dramatically higher survival rate estimates than those stocked in other years. Only stocking reach GR1 appreciably affected 1st-interval survival of stocked razorback suckers: tank- and pond- reared fish survived at higher rates when stocked there than when stocked into CO2 or GU2. Subsequent-interval survival rate estimates were higher for razorback suckers stocked from 2004–2007 than for those stocked from 1995–2005, and also higher than the assumed adult survival rate in the integrated stocking plan.

Recapture probabilities were higher for a fish's first occasion in the river after stocking than for subsequent occasions, but were all generally low. Pond-reared razorback suckers had highest predicted recapture probabilities (1st- or subsequent-intervals), followed by intensively-reared and tank-reared fish, in descending order. Recapture probabilities were highest in 2008, when most sampling effort occurred in the basin, and for razorback suckers stocked into reaches CO2 and GU2. We were unable to estimate a useful relationship between recapture probabilities and total length at stocking, but fish stocked at larger sizes were recaptured in higher proportions than those at which they were stocked.

Given the positive relationship between size at stocking and survival rate estimates and the constraints under which razorback sucker rearing facilities operate, a cost-benefit analysis is necessary to quantify the trade-offs (more space, food, and time) of growing fish of adequate size to meet razorback sucker recovery goals. Coupling results of such an analysis with an optimal study design would allow future parameter estimation analyses to better quantify the effects of primary factors of interest (rearing methods, stocking protocols, environmental variables). For example, efficacy of continued stocking of tank-reared razorback suckers would be best evaluated by stocking similar numbers of those fish into the same reach across different seasons. Instituting a standardized stocking protocol which employs what has been learned from this and other studies may be prudent as numerous rearing facilities expand to full production capacity.

RECOMMENDATIONS

- Cease stocking of razorback suckers during summer months.
- Increase recommended total length at stocking of razorback suckers.
- Conduct a cost-benefit analysis of razorback sucker total length at stocking, season of stocking, rearing method, and associated 1st-interval survival.

- Collect individual weight data on at least a subsample of every batch of stocked razorback suckers. Resulting length-weight relationships would provide a "condition factor" that may aid in future predictions of survival and comparisons among treatment groups.
- Investigate reasons for low 1st-interval survival of stocked razorback suckers (predation, acclimation, lack of conditioning).
- Incorporate these results into the razorback sucker monitoring program under development, which includes early life stages as well as adults. Minimally, the monitoring program should assist with increasing recapture probabilities by employing sampling efforts designed to maximize capture of razorback suckers.
- Evaluate changes to the integrated stocking plan for razorback suckers with a standardized stocking program and continued survival rate estimation. Analyses must employ an optimal study design in order to estimate effects of important variables, such as rearing method, reach of stocking, and season of stocking.
- Improve assessment of progress toward razorback sucker recovery using population trend analyses, in addition to minimum subbasin population size targets already defined in the species' recovery goals.

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Table 1. Releases and recaptures of hatchery-reared razorback suckers reared by three methods and stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007. Releases include any fish recaptured from previous years and re-released.

Releases		Recaptures				
Year	Number	2005	2006	2007	2008	Total
			tank			
2004	0	0	0	0	0	0
2005	6128		6	2	1	9
2006	6880			2	1	3
2007	6498				0	0
Total	19506	0	6	4	2	12
			pond			
2004	7722	224	44	40	72	380
2005	8610		170	48	102	320
2006	9179			66	68	134
2007	7263				204	204
Total	32774	224	214	154	446	1038
			intensive			
2004	14007	70	74	44	57	245
2005	2987		22	5	2	29
2006	15191			50	31	81
2007	12848				106	106
Total	45033	70	96	99	196	461
Total	97313	294	316	257	644	1511

Table 2. Number and total lengths (TL) of razorback suckers stocked per rearing method, year, and season in the Upper Colorado River Basin, Utah and Colorado, 2004–2007. Spring = March, April, and May; summer = June, July, and August; autumn = September and October; winter = November and December.

Season of stocking	Length at stocking (mm TL)		Year of stocking				total
	mean	range	2004	2005	2006	2007	
			tank				
spring	380.4	(325–490)	0	0	3	2	5
summer	295.2	(142–411)	0	6128	5735	6457	18320
autumn	315.1	(212–442)	0	0	1136	35	1171
winter			0	0	0	0	0
total	296.4	(142–490)		6128	6874	6494	19496
			pond				
spring	307.3	(195–439)	458	0	0	0	458
summer	304.9	(147–513)	1808	1769	1638	460	5675
autumn	309.8	(117–530)	5456	6472	7327	5729	24984
winter	324.0	(200–430)	0	146	0	920	1066
total	309.4	(117–530)	7722	8387	8965	7109	32183
			intensive				
spring	324.4	(220–497)	801	255	0	398	1454
summer	309.1	(206–560)	2103	823	6319	2578	11823
autumn	293.8	(170–464)	9196	1188	8777	9773	28934
winter	279.5	(200–360)	1907	651	0	0	2558
total	298.0	(170–560)	14007	2917	15096	12749	44769
overall	301.5	(117–560)	21729	17432	30935	26352	96448

Table 3. Number and total lengths (TL) of razorback suckers stocked per rearing method and year in five reaches of the Upper Colorado River Basin, Utah and Colorado, 2004–2007. CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; GU2 = Gunnison River, >RK 4.9; GR3 = Green River, RK 347.8 – 540.0; GR2 = Green River, RK 206.1 – 347.7; GR1 = Green River, RK 0.0 – 206.0.

Reach of stocking	Length at stocking (mm TL)		Year of stocking				total
	mean	range	2004	2005	2006	2007	
			tank				
CO2	295.1	(174–490)		4487	3264	2564	10315
GU2	304.3	(142–400)		0	1136	864	2000
GR3							
GR2							
GR1	296.1	(160–411)		1641	2474	3066	7181
total	296.4	(142–490)		6128	6874	6494	19496
			pond				
CO2	311.4	(117–530)	6153	5797	4430	5056	21436
GU2	287.9	(124–516)	0	0	1896	1580	3476
GR3							
GR2							
GR1	313.6	(171–434)	1569	2590	2639	473	7271
total	309.4	(117–530)	7722	8387	8965	7109	32183
			intensive				
CO2							
GU2							
GR3	300.3	(185–560)	9619	2917	5021	7749	25306
GR2	290.2	(170–385)	0	0	10075	0	10075
GR1	300.2	(200–464)	4388	0	0	5000	9388
total	298.0	(170–560)	14007	2917	15096	12749	44769
overall	301.5	(117–560)	21729	17432	30935	26352	96448

Table 4. Lengths at stocking of hatchery-reared razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007.

Year of stocking	Length at stocking (mm TL)	
	Mean	Range
2004	305	(164–510)
2005	304	(174–560)
2006	293	(124–517)
2007	307	(117–516)
total	301.5	(117–560)

Table 5. Recaptures of hatchery-reared razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007.

Year of stocking	Year of recapture				total	%
	2005	2006	2007	2008		
2004	294	118	86	145	643	43
2005		198	58	111	367	24
2006			113	94	207	14
2007				294	294	19
total	294	316	257	644	1511	100
%	19	21	17	43	100	

Table 6. Recaptures, per season and year of stocking, of individual razorback suckers reared by three methods and stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007. Spring = March, April, and May; summer = June, July, and August; autumn = September and October; winter = November and December.

Season of stocking	Year of stocking				total	% of total recaptures
	2004	2005	2006	2007		
			tank			
spring						
summer		9	3		12	0.8
autumn						
winter						
total		9	3		12	0.8
			pond			
spring	33				33	2.2
summer	23	5		2	30	2.0
autumn	324	289	121	159	893	60.7
winter		18		29	47	3.2
total	380	312	121	190	1003	68.2
			intensive			
spring	36	5		1	42	2.9
summer	4	6	18	18	46	3.1
autumn	205	13	61	85	364	24.8
winter		3			3	0.2
total	245	27	79	104	455	31.0
overall	625	348	203	294	1470	100.0

Table 7. Recaptures, per reach and year of stocking, of individual razorback suckers reared by three methods and stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007. CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; GU2 = Gunnison River, >RK 4.9; GR3 = Green River, RK 347.8 – 540.0; GR2 = Green River, RK 206.1 – 347.7; GR1 = Green River, RK 0.0 – 206.0.

Reach of stocking	Year of stocking				total	% of total recaptures
	2004	2005	2006	2007		
			tank			
CO2		1	1		2	0.1
GU2						
GR3						
GR2						
GR1		8	2		10	0.7
total		9	3		12	0.8
			pond			
CO2	287	63	37	138	525	35.7
GU2			1	39	40	2.7
GR3						
GR2						
GR1	93	249	83	13	438	29.8
total	380	312	121	190	1003	68.2
			intensive			
CO2						
GU2						
GR3	164	27	44	47	282	19.2
GR2			35		35	2.4
GR1	81			57	138	9.4
total	245	27	79	104	455	31.0
overall	625	348	203	294	1470	100.0

Table 8. Cormack-Jolly-Seber open population models to estimate apparent survival (φ) and recapture probability (*p*) for hatchery-reared razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007. The top seven models selected by AIC_C values are shown for comparison. AIC_c = Akaike's Information Criterion, adjusted for small sample size bias; Delta AIC_c = AIC_c – minimum AIC_c; AIC_c Weight = ratio of delta AIC_c relative to entire set of candidate models; Model Likelihood = ratio of AIC_c weight relative to AIC_c weight of best model; *K* = number of parameters; Deviance = log-likelihood of the model – log-likelihood of the saturated model. Effects included: group or rearing method (*g*), time (*t*), 1st interval or occasion in the river (ry1), season of stocking (seas), reach of stocking (reach), and total length at stocking (TL, TL^2).

Model	AIC*c*	Delta AIC*c*	AIC*c* Weights	Model Likelihood	*K*	Deviance
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	15855.734	0	0.81	1.000	29	15797.72
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(t+ry1+reach1+TL,TL^2)}	15859.318	3.584	0.14	0.167	27	15805.30
{phi(g+t+ry1+seas+reachALL+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	15861.166	5.432	0.05	0.066	28	15805.15
{phi(t+ry1+seas+reach1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	15889.940	34.207	0	0	26	15837.93
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+t+ry1+reach1)}	15898.093	42.359	0	0	27	15844.08
{phi(t+ry1+seas+reachALL+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	15901.425	45.692	0	0	26	15849.41
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(t+ry1+reach1)}	15903.258	47.524	0	0	24	15855.25

Table 9. Parameter estimates and 95% confidence limits for the function of logit φ, survival rate, of hatchery-reared razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007. Tank and pond = rearing methods (groups); 2004–2005, 2005–2006, and 2006–2007 = survival intervals; ry1 = effect of 1st interval in the river (vs. subsequent intervals); spring (March, April, and May), summer (June, July, and August), autumn (September and October), winter (November and December) = categorical covariates; CO2 (Colorado River, RK 200.1–303.2, plus Gunnison River, RK 0.0–4.9), GU2 (Gunnison River, >RK 4.9), GR3 (Green River, RK 347.8–540.0), GR2 (Green River, RK 206.1–347.7) = categorical covariates; TL and TL^2 (total length at stocking) = individual covariates. The intercept represents intensively-reared razorback suckers through interval 2007–2008. The ry1 effect acts as an intercept for covariates and represents fish stocked during spring into reach GR1 (Green River, RK 0.0–206.0).

Parameter	Beta	95% Confidence Limits	
intercept	1.43	0.45	2.41
tank	1.41	-1.44	4.26
pond	1.10	0.20	2.00
2004-2005	1.37	0.87	1.86
2005-2006	-0.01	-0.43	0.41
2006-2007	-0.33	-0.68	0.03
ry1	-10.67	-15.33	-6.02
summer	-2.33	-2.88	-1.78
autumn	-0.67	-1.14	-0.20
winter	-1.66	-2.28	-1.05
CO2	-2.64	-3.09	-2.19
GU2	-2.79	-3.91	-1.68
GR3	-0.46	-0.90	-0.03
GR2	-0.71	-1.54	0.12
TL	0.03	0.00	0.06
TL^2	-0.00001	-0.00006	0.00003

Table 10. Parameter estimates and 95% confidence limits for the function of logit *p*, recapture probability, of hatchery-reared razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007. Tank and pond = rearing methods (groups); 2005, 2006, and 2007 = recapture occasions; ry1 = effect of 1st occasion in the river (vs. subsequent occasions); CO2 (Colorado River, RK 200.1–303.2, plus Gunnison River, RK 0.0–4.9), GU2 (Gunnison River, >RK 4.9), GR3 (Green River, RK 347.8–540.0), GR2 (Green River, RK 206.1–347.7) = categorical covariates; TL and TL^2 (total length at stocking) = individual covariates. The intercept represents intensively-reared razorback suckers on occasion 2008. The ry1 effect acts as an intercept for covariates and represents fish stocked into reach GR1 (Green River, RK 0.0–206.0).

Parameter	Beta	95% Confidence Limits	
intercept	-3.52	-4.01	-3.03
tank	-2.22	-4.74	0.29
pond	0.66	0.10	1.22
2005	-1.20	-1.64	-0.76
2006	-0.54	-0.85	-0.24
2007	-0.82	-1.03	-0.60
ry1	0.57	-3.17	4.31
CO2	1.40	1.07	1.73
GU2	1.22	0.12	2.33
GR3	0.01	-0.35	0.38
GR2	0.71	-0.13	1.55
TL	0.01	-0.01	0.03
TL^2	-0.00003	-0.000059	0.000003

Table 11. Razorback suckers reared by three methods, stocked per season (2004–2007), and subsequently recaptured (2005–2008) in the Upper Colorado River Basin, Utah and Colorado. Spring = March, April, and May; summer = June, July, and August; autumn = September and October; winter = November and December.

Season of stocking	number stocked	number recaptured	% recaptured
		tank	
spring	5		0
summer	18320	12	0.07
autumn	1171		0
winter			
all	19496	12	0.06
		pond	
spring	458	33	7.21
summer	5675	30	0.53
autumn	24984	893	3.57
winter	1066	47	4.41
all	32183	1003	3.12
		intensive	
spring	1454	42	2.89
summer	11823	46	0.39
autumn	28934	364	1.26
winter	2558	3	0.12
all	44769	455	1.02
total	96448	1470	1.52

Table 12. Razorback suckers stocked per year (2004–2007) and subsequently recaptured (2005–2008) in the Upper Colorado River Basin, Utah and Colorado.

Year of stocking	Number stocked	Number recaptured	Recaptures	
			% of year	% of recaps
2004	21729	625	2.9	42.5
2005	17432	348	2.0	23.7
2006	30935	203	0.7	13.8
2007	26352	294	1.1	20.0
total	96448	1470		100.00

Table 13. Razorback suckers reared by three methods and stocked into reach GR1 (Green River, RK 0.0 – 206.0) per year and season.

Season of stocking	Year of stocking 2004	2005	2006	2007
		tank		
spring				
summer		1641	2474	3066
autumn				
winter				
		pond		
spring				
summer				
autumn	1569	2444	2639	
winter		146		473
		intensive		
spring				
summer				1923
autumn	2481			3077
winter	1907			

Table 14. Predicted results of stocking 300 mm TL razorback suckers into the Upper Colorado River Basin under current stocking levels compared to approximate levels required to meet adult population goals, using mean survival rates estimated in this analysis. Mean 1st-interval and subsequent-interval survival rates were calculated from pond- and intensively-reared fish stocked from 2005–2007. The dotted line depicts the threshold above which fish are considered adults (age-4, 400 mm TL) and, therefore, contribute to the goal of 7,540 adults per population.

Year	Age	Mean survival rate	Current stocking level	To meet goal in 6 yrs	To meet goal in 10 yrs
1	2	0.06	9930	42900	28100
2	3	0.85	640	2763	1810
3	≥4	0.85	545	2356	1543
4	≥4	0.85	465	2009	1316
5	≥4	0.85	397	1714	1122
6	≥4	0.85	338	1461	957
7	≥4	0.85	288		816
8	≥4	0.85	246	sum 7540	696
9	≥4	0.85	210		594
10	≥4	0.85	179		506
11			153		
12			130		sum 7551
13			111		
14			95		
15			81		
16			69		
17			59		
18			50		
19			43		
20			36		
21			31		
22			26		
23			23		
24			19		
25			16		
26			14		
27			12		
28			10		
29			9		
30			7		
31			6		
32			5		
33			5		
34			4		
35			3		
36			3		
37			2		
38			2		
39			2		
40			2		
		sum	3696		

Table 15. Predicted results of stocking 400 mm TL razorback suckers into the Upper Colorado River Basin under current stocking levels, using mean survival rates estimated in this analysis. Mean 1st-interval and subsequent-interval survival rates were calculated from pond- and intensively-reared fish stocked from 2005–2007.

Year	Age	Mean survival rate	Current stocking level
1	4	0.40	9930
2	5	0.85	4017
3	6	0.85	3426
4	7	0.85	2921
5	8	0.85	2491
6	9	0.85	2124
		6-year total	24909
7	10	0.85	1812
8	11	0.85	1545
9	12	0.85	1317
10	13	0.85	1123
		10-year total	30707

Table 16. Razorback suckers reared by three methods, stocked per reach (2004–2007), and subsequently recaptured (2005–2008) in the Upper Colorado River Basin, Utah and Colorado. CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; GU2 = Gunnison River, >RK 4.9; GR3 = Green River, RK 347.8 – 540.0; GR2 = Green River, RK 206.1 – 347.7; GR1 = Green River, RK 0.0 – 206.0.

Reach of stocking	Number stocked	Number recaptured	% recaptured
	tank		
CO2	10315	2	<0.1
GU2	2000		0
GR1	7181	10	0.1
	pond		
CO2	21436	525	2.4
GU2	3476	40	1.2
GR1	7271	438	6.0
	intensive		
GR3	25306	282	1.1
GR2	10075	35	0.3
GR1	9388	138	1.5

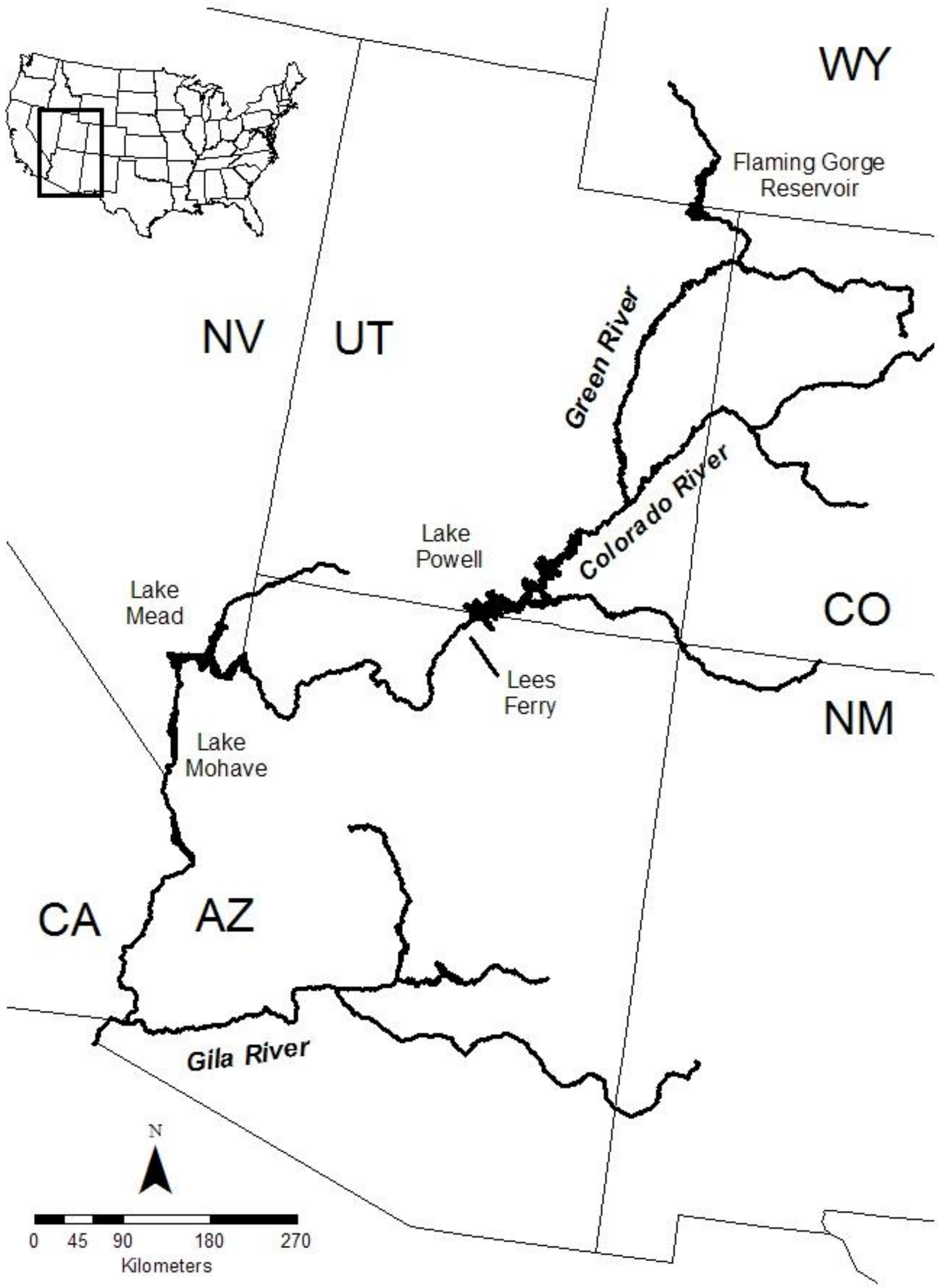

Figure 1. Map of the Colorado River Basin. Lees Ferry divides the Upper and Lower Colorado River basins.

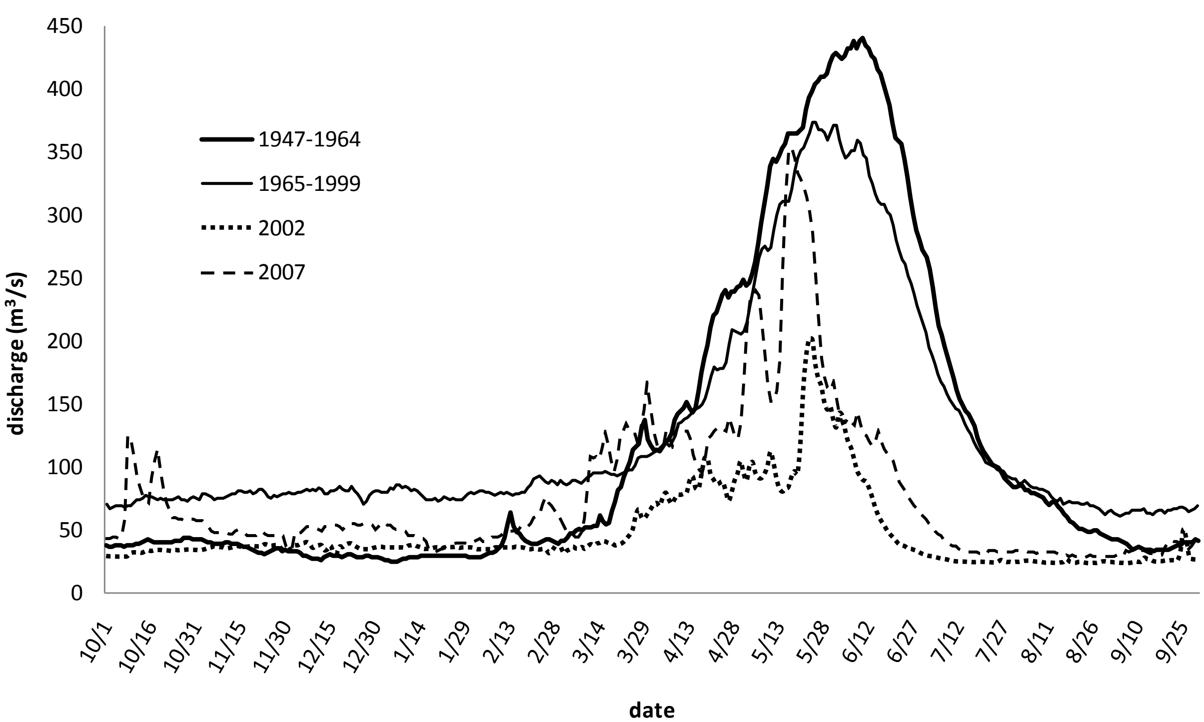

Figure 2. Mean daily discharge of the Green River near Jensen, Utah (U.S. Geological Survey gage 09261000), for water years 1947–1964 (pre-impoundment), 1965–1999 (post-impoundment) and recent low-flow years 2002 and 2007.

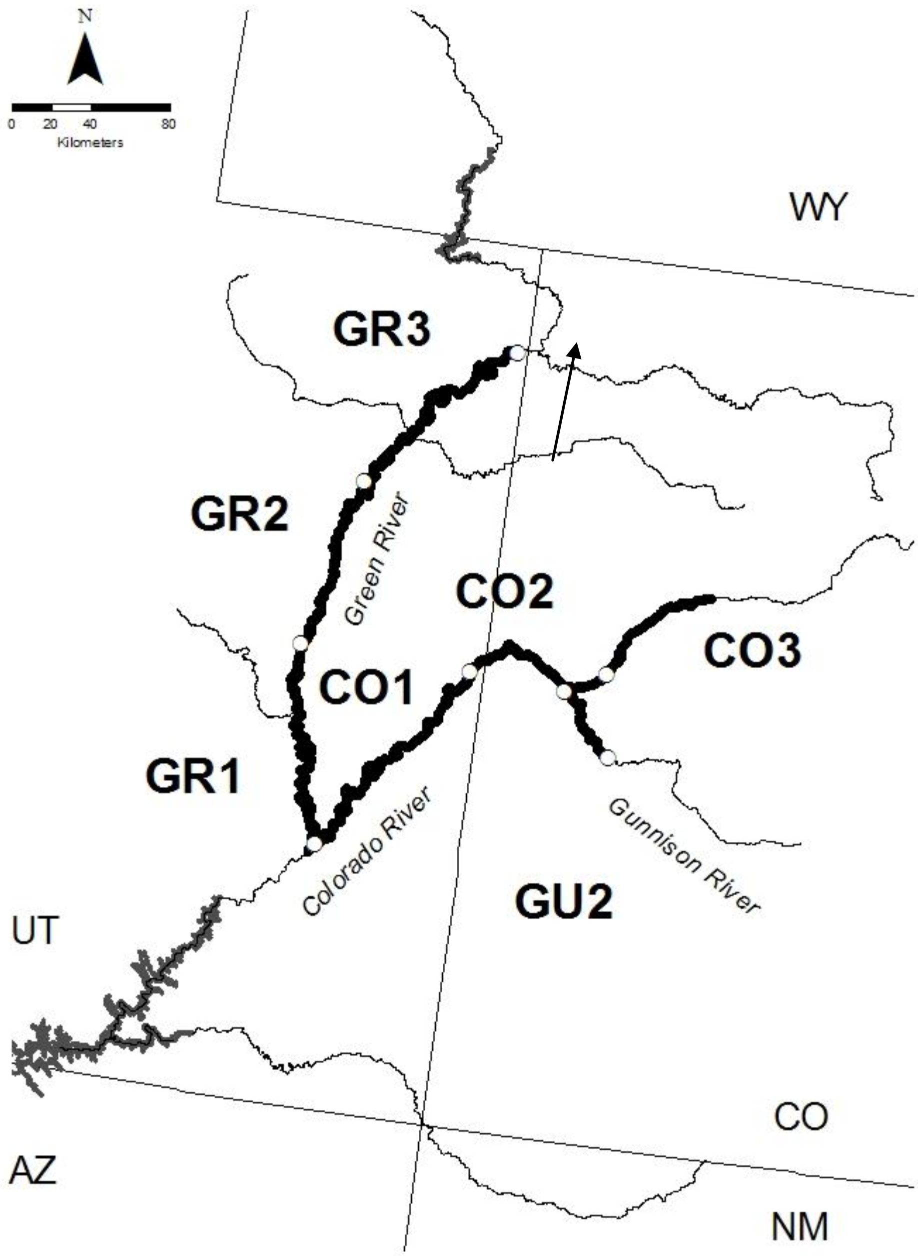

Figure 3. Study reaches within the Upper Colorado River Basin. CO1 = Colorado River, RK 0.0 – 200.0; CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; CO3 = Colorado River, RK 303.3 – 390.0; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0; GR2 = Green River, RK 206.1 – 347.7; GR3 = Green River, RK 347.8 – 540.0. Open circles denote reach boundaries.

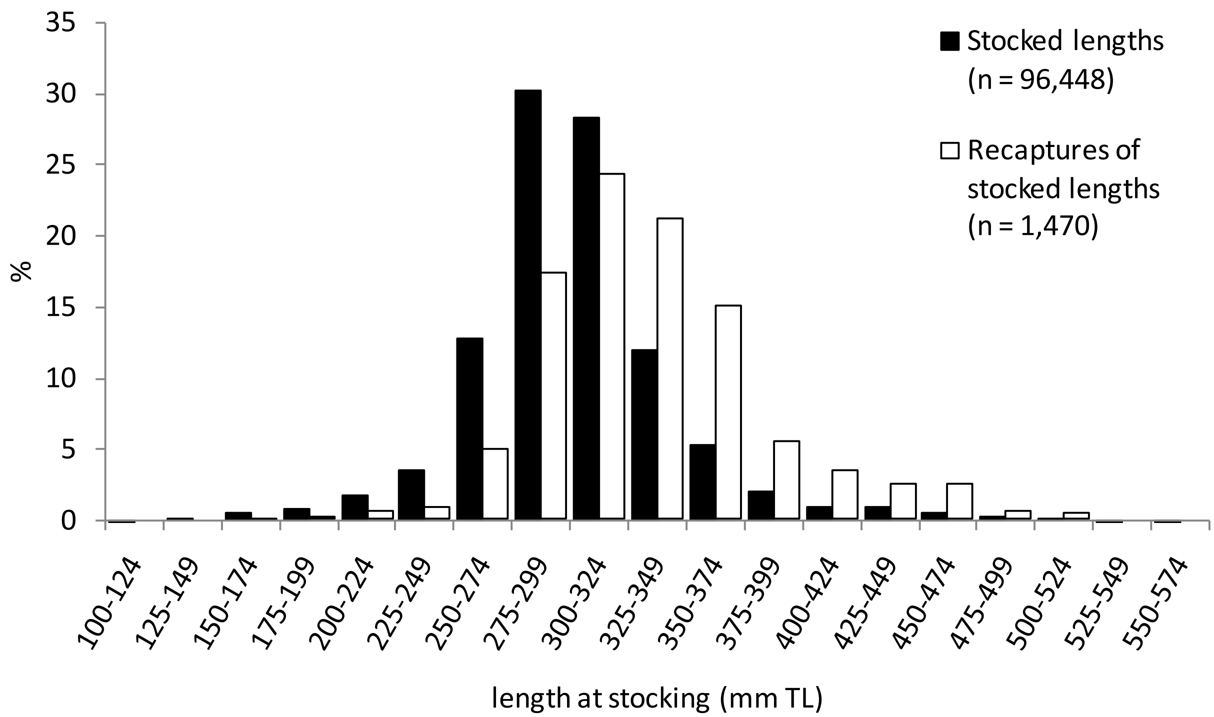

Figure 4. Length frequencies of razorback suckers stocked and subsequently recaptured in the Upper Colorado River Basin, Utah and Colorado, 2004–2007. TL = total length.

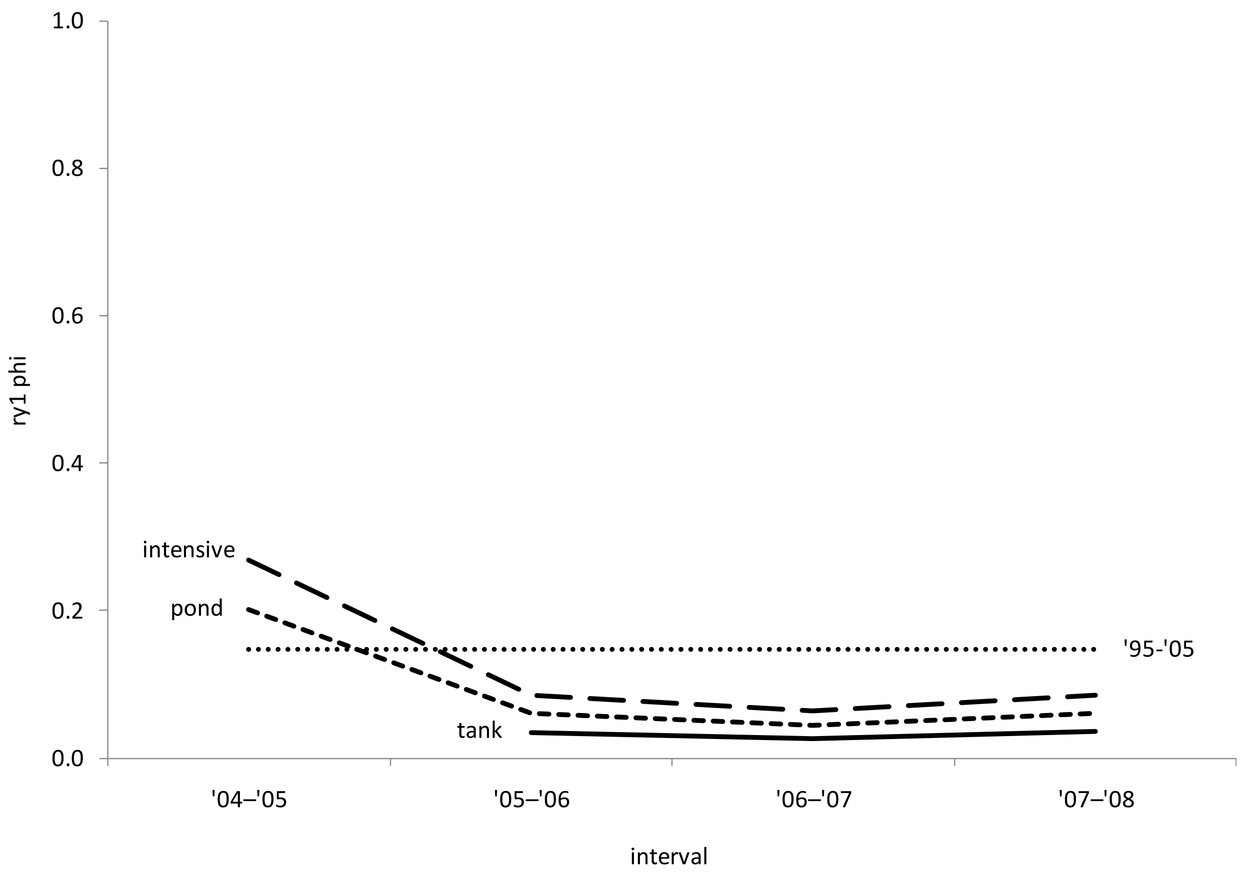

Figure 5. First-interval survival rate (ry1 phi) estimates for average-length (301.5 mm TL) razorback suckers reared by three methods and stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007, averaging across each method's seasons and reaches of stocking. See Appendix C for 95% confidence intervals. The dotted line represents the mean ry1 phi estimated for similar-sized razorback suckers stocked from 1995–2005, averaging across seasons of stocking.

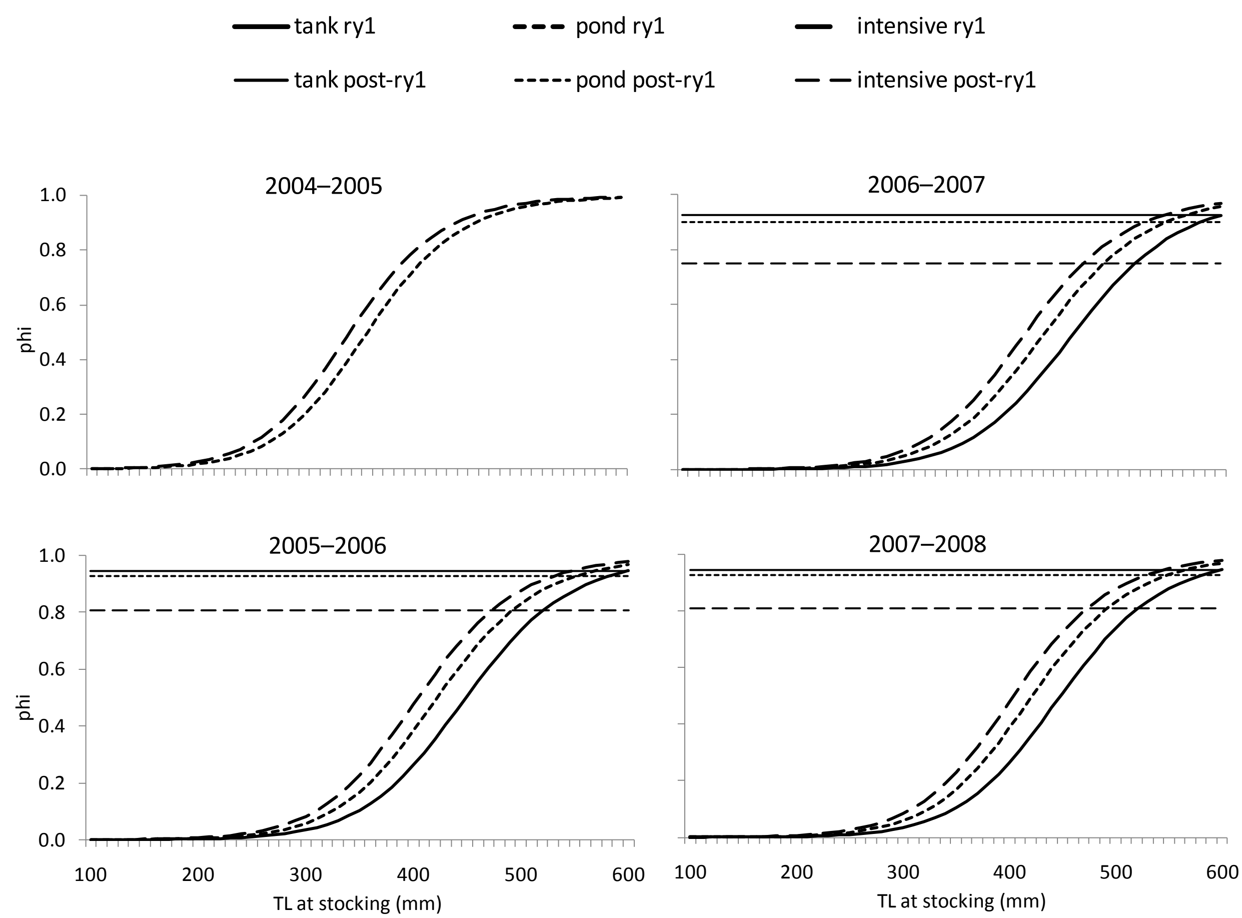

Figure 6. Total length (TL)-dependent, 1st-interval (ry1) and subsequent-interval (post-ry1) survival rate estimates for razorback suckers reared by three methods and stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007. First-interval estimates were averaged across each method's seasons and reaches of stocking. No tank-reared fish were stocked in 2004. Since this analysis began with fish stocked in 2004, there are no subsequent-interval estimates for the 2004–2005 interval.

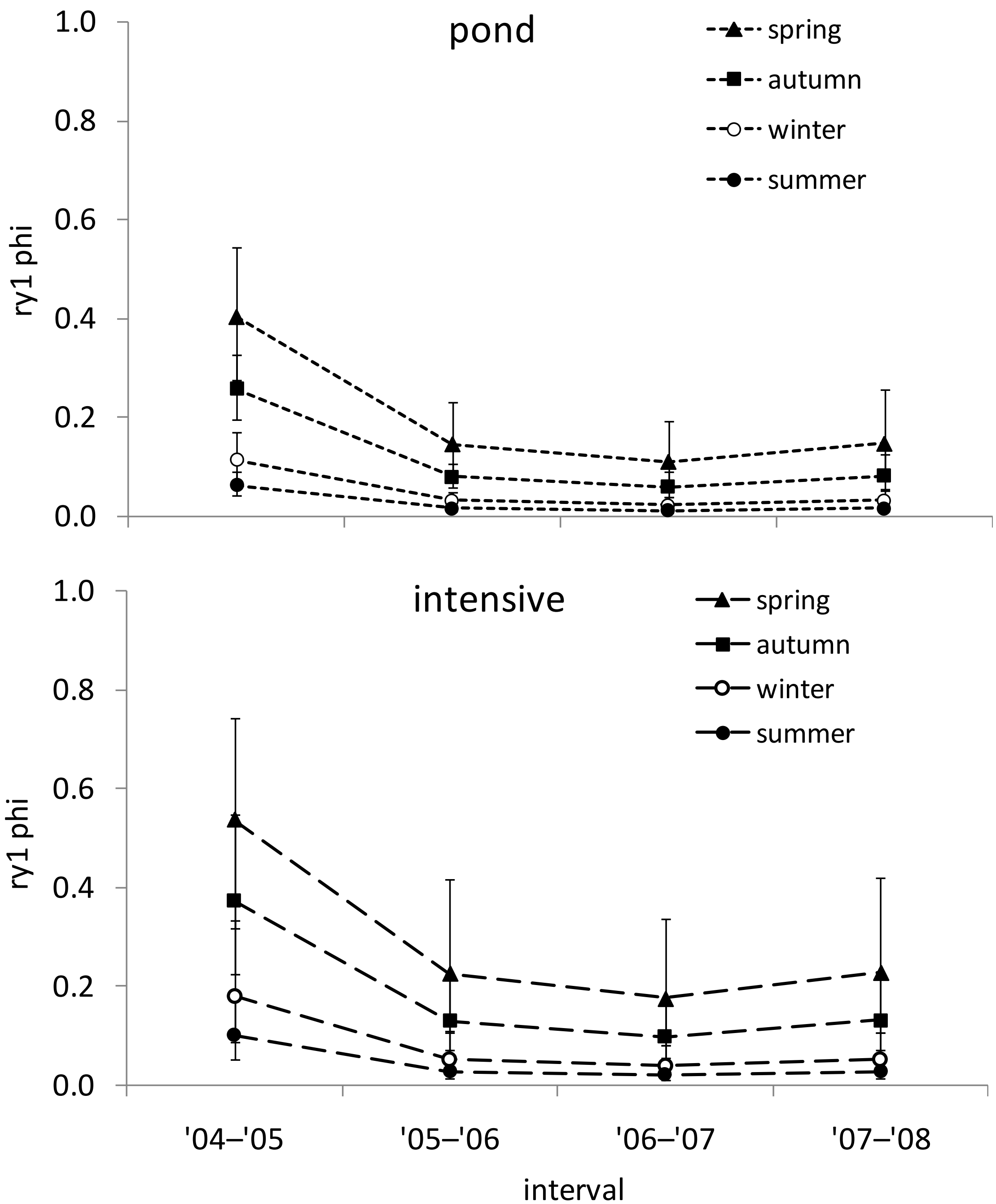

Figure 7. Seasonal, 1st-interval survival rate (ry1 phi) estimates and 95% confidence intervals for 301.5 mm total length razorback suckers reared by two methods and stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007. Spring = March, April, and May; summer = June, July, and August; autumn = September and October; winter = November and December. Estimates were calculated by averaging across each method's reaches of stocking.

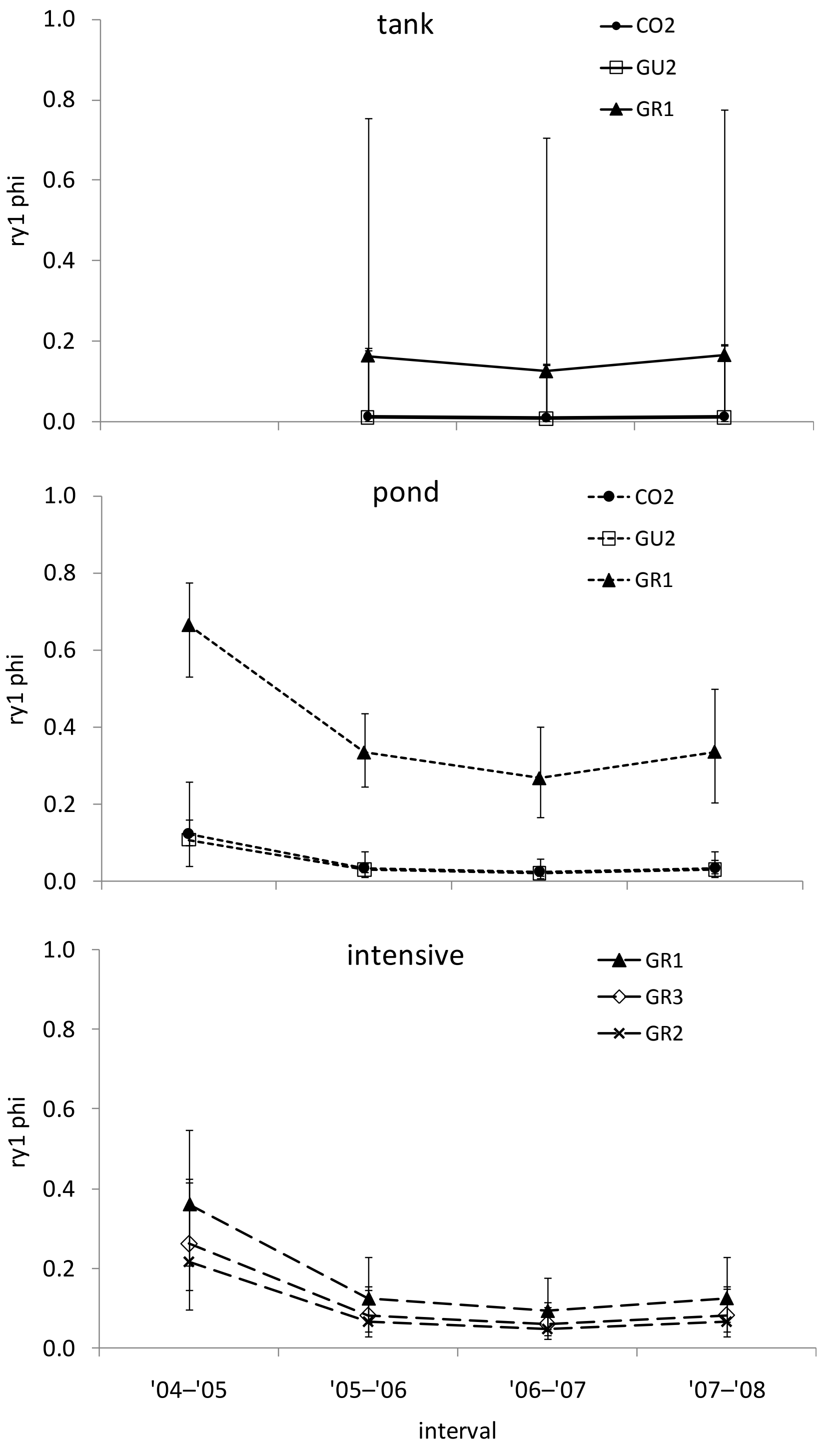

Figure 8. First-interval survival rate (ry1 phi) estimates and 95% confidence intervals for 301.5 mm total length razorback suckers reared by three methods and stocked into five reaches of the Upper Colorado River Basin, Utah and Colorado, 2004–2007. CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; GU2 = Gunnison River, >RK 4.9; GR3 = Green River, RK 347.8 – 540.0; GR2 = Green River, RK 206.1 – 347.7; GR1 = Green River, RK 0.0 – 206.0. Estimates were calculated by averaging across each method's seasons of stocking.

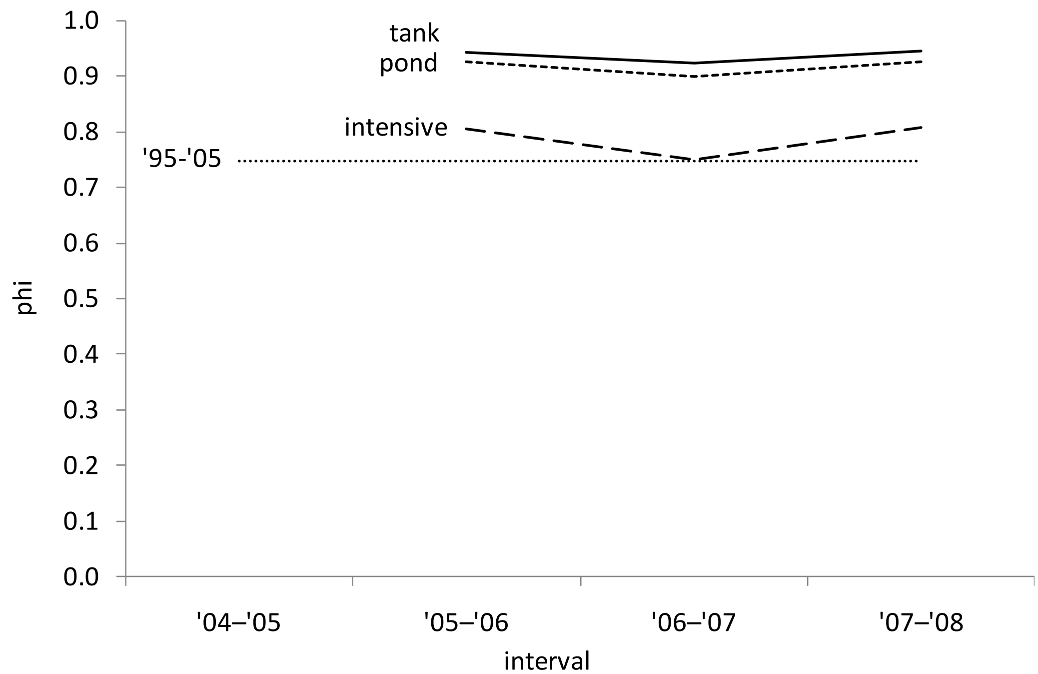

Figure 9. Survival rate (phi) estimates for razorback suckers reared by three methods and stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007, through any interval subsequent to their first intervals in river. The dotted line represents the mean subsequent-interval phi estimated for razorback suckers stocked from 1995–2005.

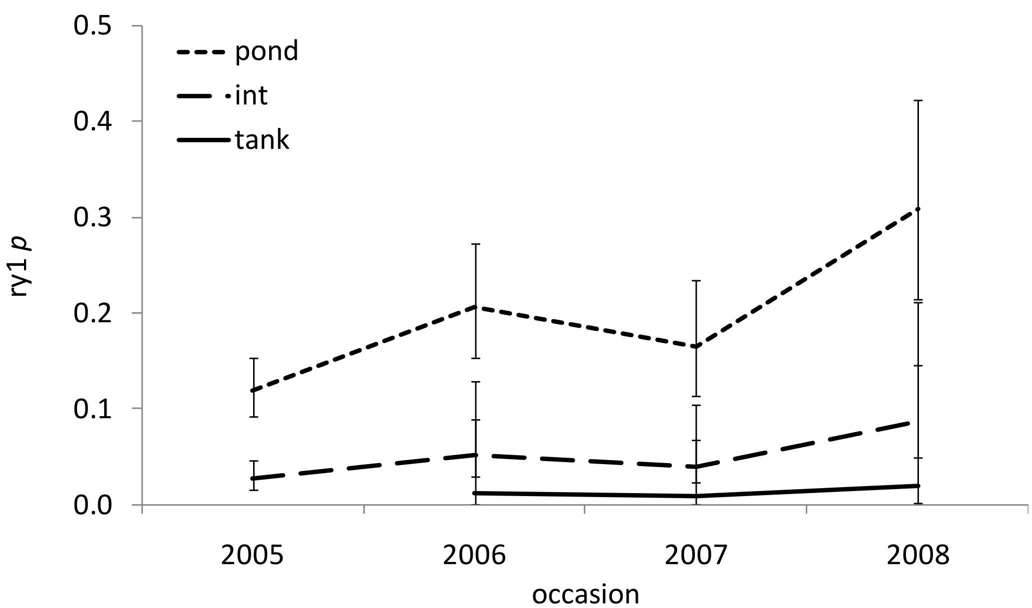

Figure 10. First-occasion recapture probability (ry1 *p*) estimates and 95% confidence intervals for 301.5 mm total length razorback suckers reared by three methods and stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007, averaging across each method's reaches of stocking. No tank-reared fish were stocked in 2004.

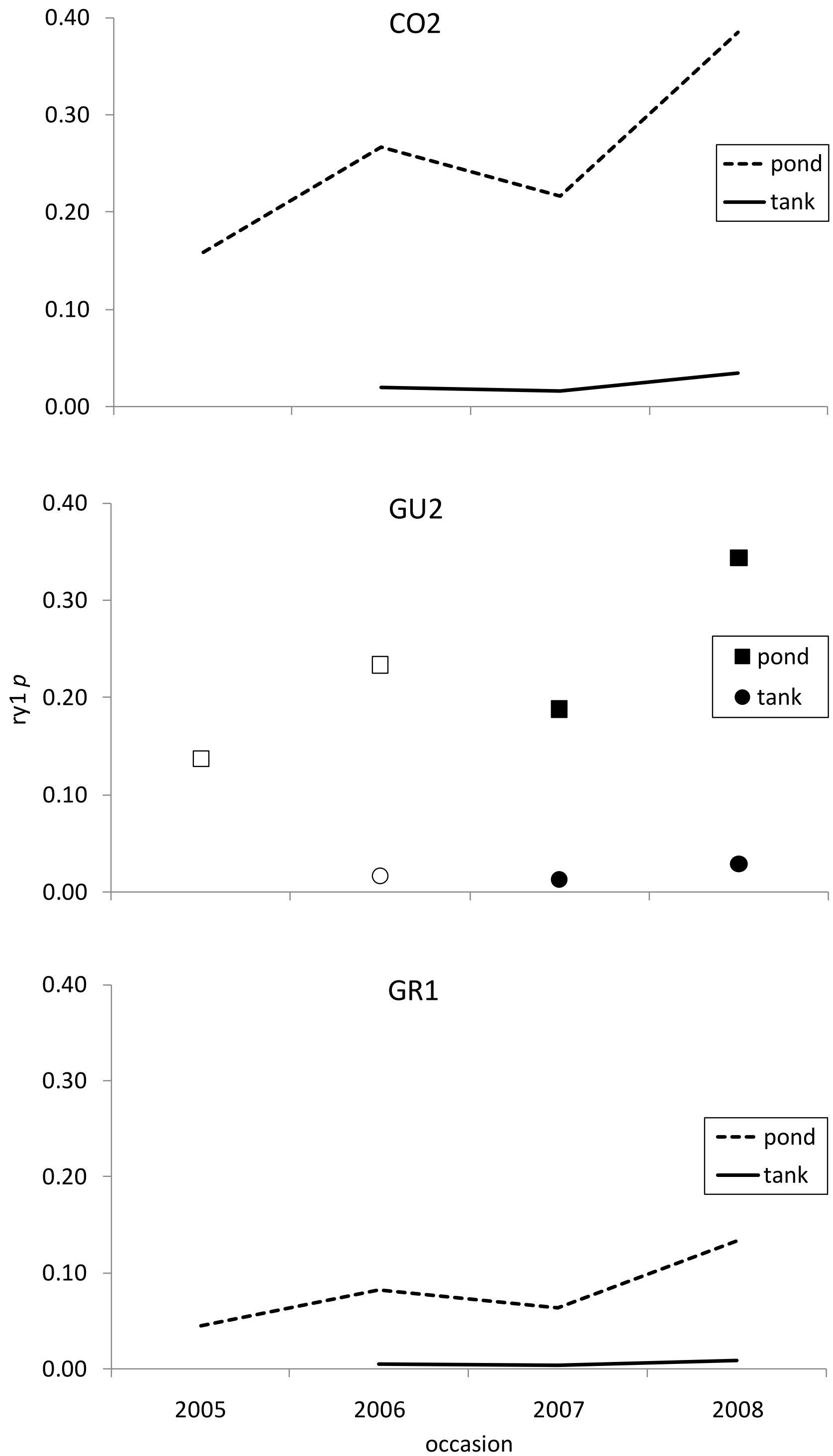

Figure 11. First-occasion recapture probability (ry1 *p*) estimates for tank- and pond-reared, 301.5 mm total length razorback suckers stocked into reaches CO2, GU2, and GR1 of the Upper Colorado River Basin, Utah and Colorado, 2004–2007. Open circles and squares denote estimates generated for occasions and reaches when no fish were previously stocked. CO2 = Colorado River, RK 200.1 – 303.2, plus Gunnison River, RK 0.0 – 4.9; GU2 = Gunnison River, >RK 4.9; GR1 = Green River, RK 0.0 – 206.0.

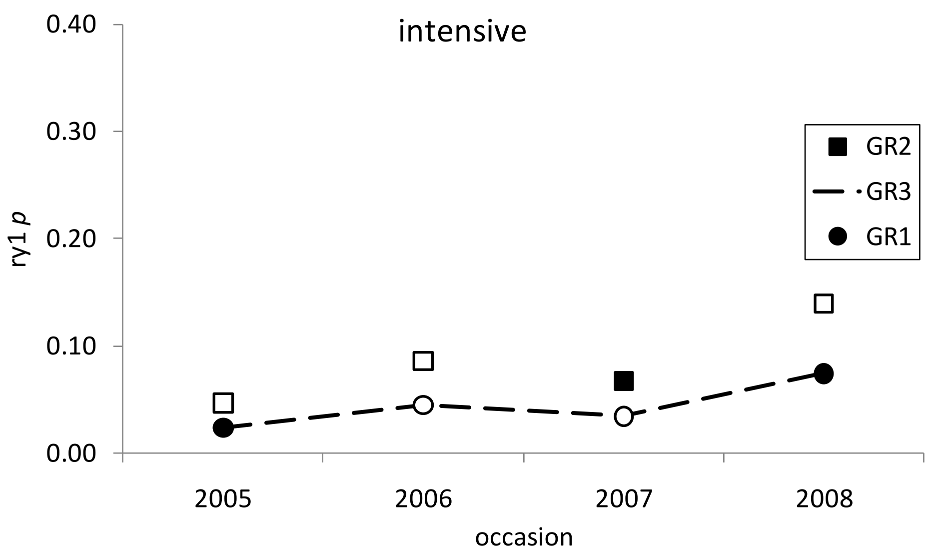

Figure 12. First-occasion recapture probability (ry1 *p*) estimates for intensively-reared, 301.5 mm total length razorback suckers stocked into reaches GR3, GR2, and GR1 of the Upper Colorado River Basin, Utah and Colorado, 2004–2007. Open circles and squares denote estimates generated for occasions and reaches when no fish were previously stocked. GR3 = Green River, RK 347.8 – 540.0; GR2 = Green River, RK 206.1 – 347.7; GR1 = Green River, RK 0.0 – 206.0.

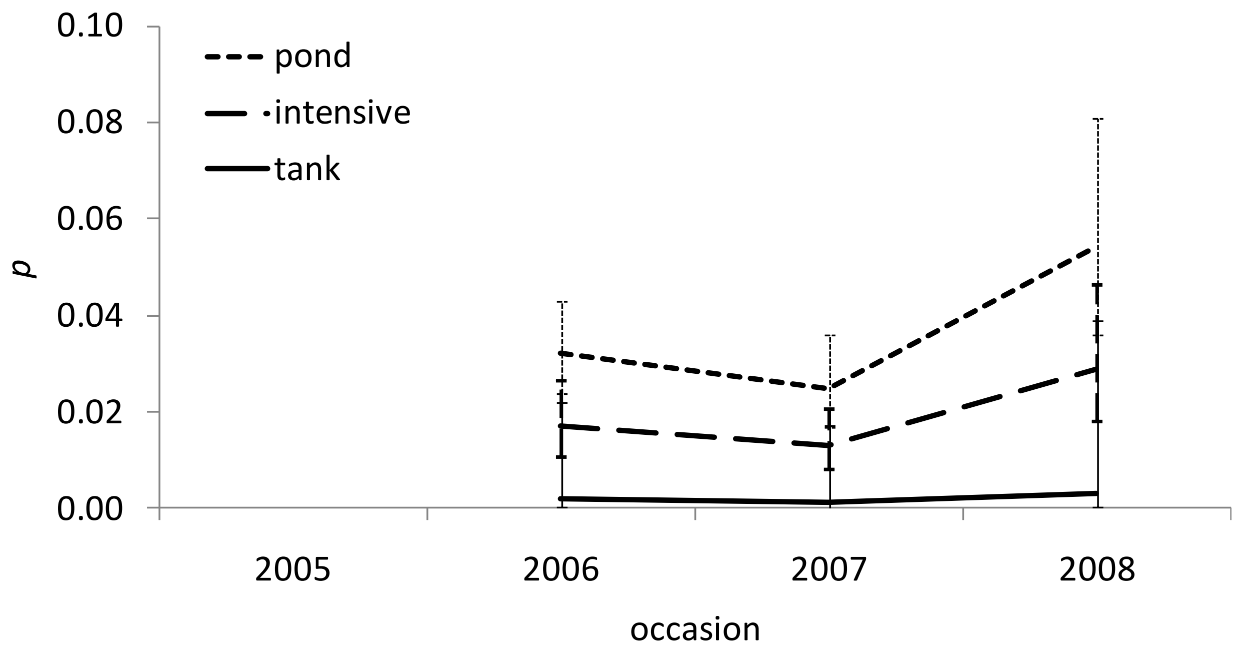

Figure 13. Recapture probability (*p*) estimates and 95% confidence intervals for razorback suckers reared by three methods and stocked into the Upper Colorado River Basin, 2004–2007, on any occasion subsequent to their first occasions in the river. Note that the scale displays a maximum of 0.10.

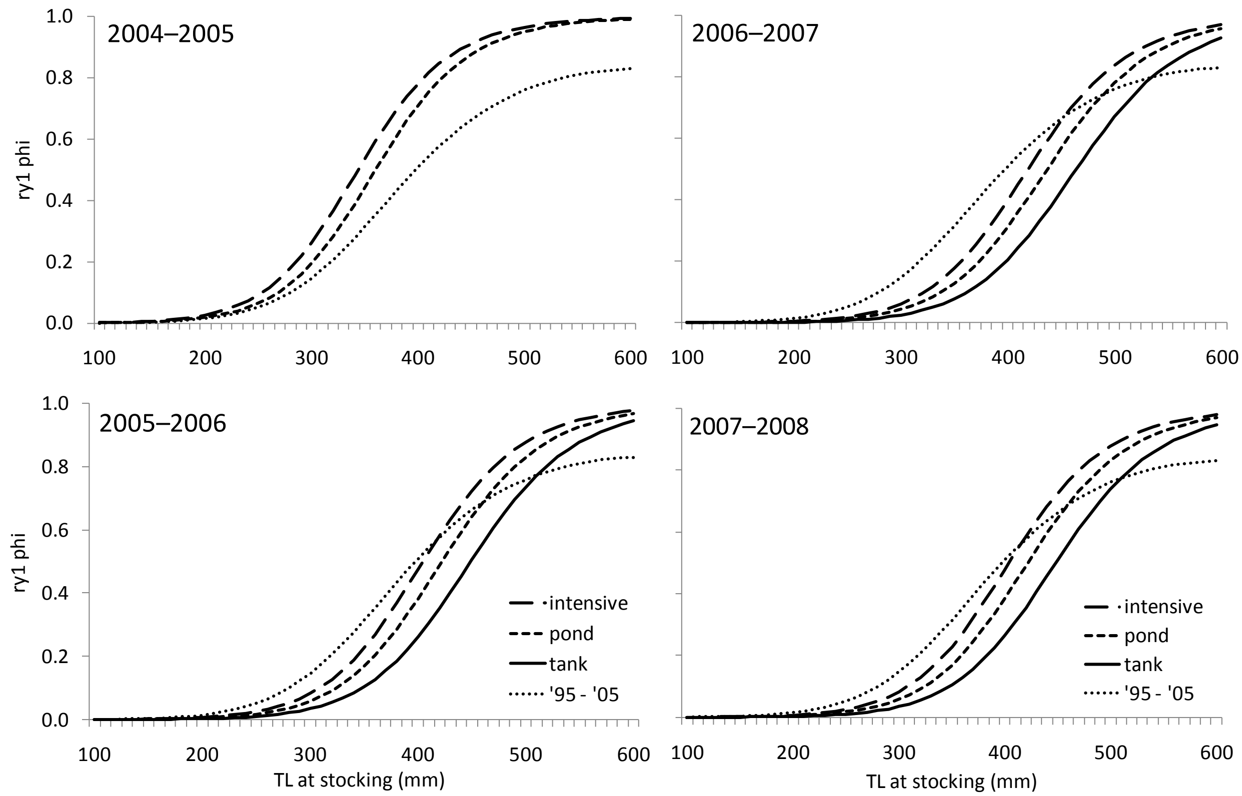

Figure 14. Total length (TL)-dependent, 1st-interval survival rate (ry1 phi) estimates for razorback suckers reared by three methods and stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007, compared to estimates for those stocked from 1995–2005. Estimates were calculated by averaging across each method's seasons and reaches of stocking. No tank-reared fish were stocked in 2004. Since this analysis began with fish stocked in 2004, there are no subsequent-interval estimates for the 2004–2005 interval.

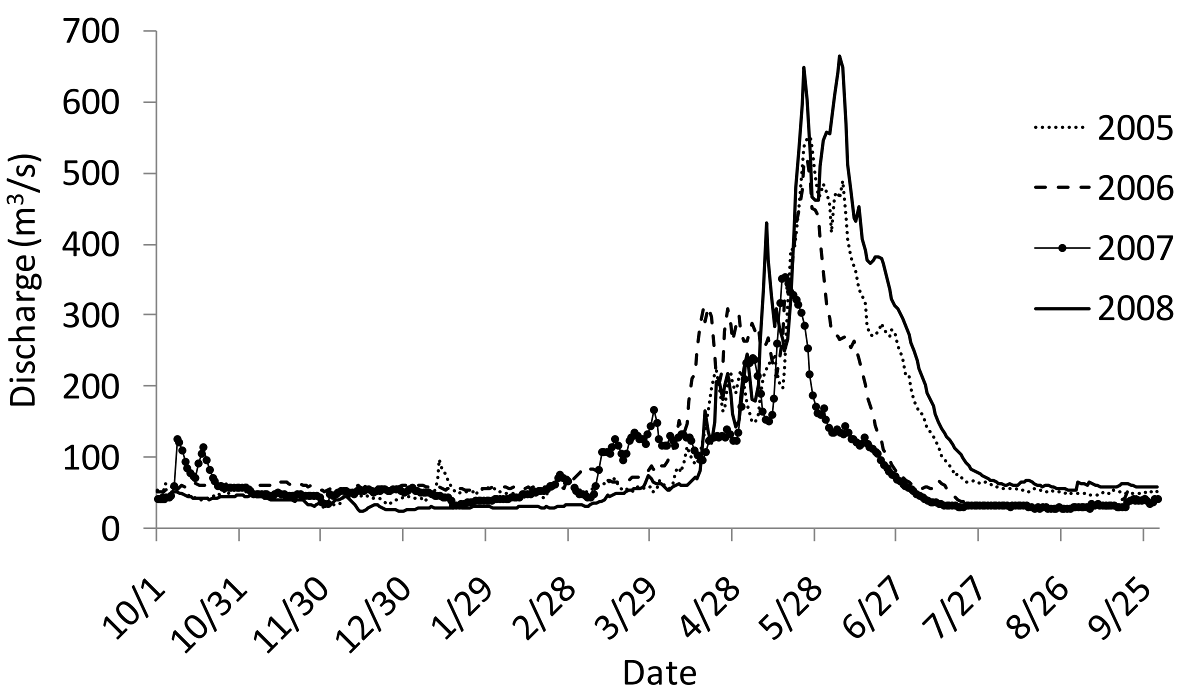

Figure 15. Mean daily discharge of the Green River near Jensen, Utah (U.S. Geological Survey gage 09261000), for water years 2005–2008.

Appendix A. A priori model structures to estimate apparent survival, φ, and recapture probability, *p*, for razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007. Effects included: no variation (.), group or rearing method (*g*), time (*t*), 1st interval or occasion in the river (ry1), season of stocking (season), reach of stocking (reach), and total length at stocking (TL, TL^2) Not all combinations of φ and *p* were analyzed.

φ structures		*p* structures
φ (.)	φ (g*t)	p (.)
φ (g)	φ (g*[t+ry1])	p (g)
φ (t)	φ (g*[t+ry1+season])	p (t)
φ (ry1)	φ (g*[t+ry1+reach1])	p (ry1)
φ (season)	φ (g*[t+ry1+reachALL])	p(reach1)
φ (reach1)	φ (g*[t+ry1+TL,TL^2])	p(reachALL)
φ (reachALL)	φ (g*[t+ry1+season+reach1])	p (TL,TL2)
φ (TL,TL2)	φ (g*[t+ry1+season+reachALL])	p(TL,TL2all)
φ (g+t)	φ (g*[t+ry1+season+TL,TL^2])	p (g+t)
φ (g+[t+ry1])	φ (g*[t+ry1+reach+TL,TL^2])	p (g+reach1)
φ (g+[t+ry1+season])	φ (g*[t+ry1+season+reach1+TL,TL^2])	p (g+reachALL)
φ (g+[t+ry1+reach1])	φ (g*[t+ry1+season+reachALL+TL,TL^2])	p (g+ry1)
φ (g+[t+ry1+reachALL])	φ (g*ry1)	p (g+[ry1+TL,TL2])
φ (g+[t+ry1+TL,TL^2])	φ (g*[ry1+season])	p (g+[ry1+reach1])
φ (g+[t+ry1+season+reach1])	φ (g*[ry1+reach1])	p (g+[ry1+reachALL])
φ (g+[t+ry1+season+reachALL])	φ (g*[ry1+reachALL])	p (g+[ry1+reach1+TL,TL2])
φ (g+[t+ry1+season+TL,TL^2])	φ (g*[ry1+TL,TL^2])	p (g+[ry1+reachALL+TL,TL2])
φ (g+[t+ry1+reach1+TL,TL^2])	φ (g*[ry1+season+reach1])	p (t+ry1)
φ (g+[t+ry1+reachALL+TL,TL^2])	φ (g*[ry1+season+reachALL])	p (t+reach1)
φ (g+[t+ry1+season+rch1+TL,TL^2])	φ (g*[ry1+season+TL,TL^2])	p (t+reachALL)
φ (g+[t+ry1+season+rchALL+TL,TL^2])	φ (g*[ry1+reach1+TL,TL^2])	p (t+ry1+TL,TL2)
φ (g+ry1)	φ (g*[ry1+reachALL+TL,TL^2])	p (t+ry1+reach1)
φ (g+[ry1+season])	φ (g*[ry1+season+reach1+TL,TL^2])	p (t+ry1+reachALL)
φ (g+[ry1+reach1])	φ (g*[ry1+season+reachALL+TL,TL^2])	p (t+ry1+reach1+TL,TL2)
φ (g+[ry1+reachALL])		p (t+ry1+reachALL+TL,TL2)
φ (g+[ry1+TL,TL^2])		p (ry1+TL,TL2)
φ (g+[ry1+season+reach1])		p (ry1+reach1)
φ (g+[ry1+season+reach]ALL)		p (ry1+reachALL)
φ (g+[ry1+season+TL,TL^2])		p (ry1+reach1+TL,TL2)
φ (g+[ry1+reach1+TL,TL^2])		p (ry1+reachALL+TL,TL2)
φ (g+[ry1+reachALL+TL,TL^2])		p (g+[t+reach1])
φ (g+[ry1+season+reach1+TL,TL^2])		p (g+[t+reachALL])
φ (g+[ry1+season+reachALL+TL,TL^2])		p (g+[t+ry1])
φ (t+ry1)		p (g+[t+ry1+TL,TL2])
φ (t+ry1+season)		p (g+[t+ry1+reach1])
φ (t+ry1+reach1)		p (g+[t+ry1+reachALL])
φ (t+ry1+reachALL)		p (g+[t+ry1+reach1+TL,TL2])
φ (t+ry1+TL,TL^2])		p (g+[t+ry1+reachALL+TL,TL2])
φ (t+ry1+season+reach1)		p (g*t)
φ (t+ry1+season+reachALL)		p (g*ry1)
φ (t+ry1+season+TL,TL^2)		p (g*[ry1+TL,TL2])
φ (t+ry1+reach1+TL,TL^2)		p (g*[ry1+reach1+TL,TL2])
φ (t+ry1+reachALL+TL,TL^2)		p (g*[ry1+reachALL+TL,TL2])
φ (t+ry1+season+reach1+TL,TL^2)		p (g*[ry1+reach1])
φ (t+ry1+season+reachALL+TL,TL^2)		p (g*[ry1+reachALL])
φ (ry1+season)		p (g*[t+ry1])
φ (ry1+reach1)		p (g*[t+ry1+TL,TL2])
φ (ry1+reachALL)		p (g*[t+ry1+reach1])
φ (ry1+TL,TL^2])		p (g*[t+ry1+reachALL])
φ (ry1+season+reach1)		p (g*[t+ry1+reach1+TL,TL2])
φ (ry1+season+reachALL)		p (g*[t+ry1+reachALL+TL,TL2])
φ (ry1+season+TL,TL^2)		
φ (ry1+reach1+TL,TL^2)		
φ (ry1+reachALL+TL,TL^2)		
φ (ry1+season+reach1+TL,TL^2)		
φ (ry1+season+reachALL+TL,TL^2)		

Appendix B. Cormack-Jolly-Seber open population models to estimate apparent survival (φ) and recapture probability (*p*) for hatchery-reared razorback suckers stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007. Effects included: no variation (.), group or rearing method (*g*), time (*t*), 1st interval or occasion in the river (ry1), season of stocking (season), reach of stocking (reach), and total length at stocking (TL and TL^2).

Model	AIC*c*	Delta AIC*c*	AIC*c* Weights	Model Likelihood	Parameters	Deviance
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	**15855.734**	**0**	**0.811**	**1.000**	**29**	**15797.716**
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(t+ry1+reach1+TL,TL^2)}	15859.318	3.584	0.135	0.167	27	15805.302
{phi(g+t+ry1+seas+reachALL+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	15861.166	5.432	0.054	0.066	28	15805.149
{phi(t+ry1+seas+reach1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	15889.940	34.207	0	0	26	15837.926
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+t+ry1+reach1)}	15898.093	42.359	0	0	27	15844.077
{phi(t+ry1+seas+reachALL+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	15901.425	45.692	0	0	26	15849.411
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(t+ry1+reach1)}	15903.258	47.524	0	0	24	15855.246
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+t+reach1)}	15920.833	65.100	0	0	25	15870.820
{phi(g+ry1+seas+reach1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	15924.483	68.750	0	0	25	15874.470
{phi(ry1+seas+reach1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	15925.843	70.109	0	0	23	15879.832
{phi(ry1+seas+reachALL+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	15925.843	70.109	0	0	23	15879.832
{phi(g+ry1+seas+reachALL+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	15926.413	70.680	0	0	26	15874.399
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+ry1+reach1+TL,TL^2)}	15927.704	71.971	0	0	26	15875.690
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+t+ry1+TL,TL^2)}	15934.440	78.706	0	0	24	15886.428
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(ry1+reach1+TL,TL^2)}	15938.308	82.574	0	0	23	15892.297
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(t+ry1+TL,TL^2)}	15942.489	86.756	0	0	22	15898.479
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+ry1+reach1)}	15951.119	95.385	0	0	24	15903.107
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+t+ry1)}	15953.773	98.039	0	0	23	15907.762
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(t+ry1)}	15959.588	103.854	0	0	20	15919.579
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(ry1+reach1)}	15962.401	106.667	0	0	21	15920.391
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+reach1)}	15963.631	107.898	0	0	22	15919.621
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(reach1)}	15978.048	122.314	0	0	20	15938.039
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+ry1+TL,TL^2)}	15990.702	134.969	0	0	22	15946.692
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+t) initial p int -2 p t's 0}	15993.734	138.001	0	0	22	15949.724
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+ry1)}	15994.061	138.327	0	0	20	15954.052
{phi(g+t+ry1+seas+reachALL+TL,TL^2) p(TL,TL^2)}	16012.589	156.855	0	0	18	15976.582
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(ry1+TL,TL^2)}	16012.722	156.988	0	0	19	15974.714
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g)}	16017.079	161.345	0	0	19	15979.071
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(ry1)}	16019.372	163.638	0	0	17	15985.366
{phi(t+ry1+reachALL+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16060.666	204.932	0	0	24	16012.654
{phi(t+ry1+seas+reachALL) p(g+t+ry1+reach1+TL,TL^2)}	16061.297	205.563	0	0	23	16015.286
{phi(g+t+ry1+reachALL+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16062.580	206.847	0	0	25	16012.567
{phi(g+t+ry1+seas+reachALL) p(g+t+ry1+reach1+TL,TL^2)}	16064.568	208.835	0	0	25	16014.555
{phi(t+ry1+seas+reach1) p(g+t+ry1+reach1+TL,TL^2)}	16071.552	215.818	0	0	24	16023.540
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(t) initial p int -2 p t's 0}	16076.073	220.339	0	0	19	16038.065
{phi(g+t+ry1+seas+reach1) p(g+t+ry1+reach1+TL,TL^2)}	16078.399	222.666	0	0	26	16026.385
{phi(g+t+ry1+reach1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16079.804	224.071	0	0	25	16029.791
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(t+reach1)}	16081.858	226.124	0	0	23	16035.847
{phi(g+ry1+seas+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16085.503	229.769	0	0	21	16043.493
{phi(ry1+seas+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16087.538	231.804	0	0	19	16049.530
{phi(t+ry1+reach1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16093.214	237.480	0	0	23	16047.203
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(g+t)}	16097.332	241.598	0	0	21	16055.322
{phi(g+t+ry1+seas+reachALL+TL,TL^2) p(reachALL)}	16115.421	259.687	0	0	20	16075.412
{phi(g+t+ry1+seas+reachALL+TL,TL^2) p(TL,TL^2all)}	16115.944	260.210	0	0	19	16077.936
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(t)}	16127.616	271.882	0	0	19	16089.608
{phi(g+t+ry1+seas+reach1+TL,TL^2) p(.)}	16141.354	285.620	0	0	17	16107.348
{phi(g+ry1+seas+reachALL) p(g+t+ry1+reach1+TL,TL^2)}	16152.565	296.832	0	0	22	16108.555
{phi(g+ry1+seas+reach1) p(g+t+ry1+reach1+TL,TL^2)}	16152.565	296.832	0	0	22	16108.555
{phi(g+ry1+reach1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16155.943	300.210	0	0	22	16111.933
{phi(g+ry1+reachALL+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16155.944	300.211	0	0	22	16111.934
{phi(ry1+reachALL+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16157.215	301.481	0	0	20	16117.206
{phi(ry1+reach1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16157.216	301.482	0	0	20	16117.207
{phi(ry1+seas+reach1) p(g+t+ry1+reach1+TL,TL^2)}	16178.184	322.450	0	0	21	16136.174
{phi(g+t+ry1+seas+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16184.614	328.880	0	0	24	16136.602
{phi(t+ry1+reachALL) p(g+t+ry1+reach1+TL,TL^2)}	16187.660	331.926	0	0	20	16147.651

Appendix B. Continued.

Model	AIC*c*	Delta AIC*c*	AIC*c* Weights	Model Likelihood	Parameters	Deviance
{phi(g+t+ry1+reachALL) p(g+t+ry1+reach1+TL,TL^2)}	16189.568	333.834	0	0	21	16147.558
{phi(ry1+seas+reachALL) p(g+t+ry1+reach1+TL,TL^2)}	16207.503	351.769	0	0	21	16165.493
{phi(t+ry1+reach1) p(g+t+ry1+reach1+TL,TL^2)}	16244.702	388.968	0	0	21	16202.692
{phi(g+t+ry1+reach1) p(g+t+ry1+reach1+TL,TL^2)}	16245.117	389.383	0	0	23	16199.106
{phi(t+ry1+seas+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16293.594	437.861	0	0	22	16249.584
{phi(g+t+ry1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16337.265	481.532	0	0	22	16293.255
{phi(g+t+ry1+seas) p(g+t+ry1+reach1+TL,TL^2)}	16342.203	486.469	0	0	21	16300.193
{phi(ry1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16381.857	526.123	0	0	16	16349.851
{phi(ry1+seas) p(g+t+ry1+reach1+TL,TL^2)}	16382.716	526.982	0	0	17	16348.710
{phi(seas) p(g+t+ry1+reach1+TL,TL^2)}	16383.128	527.394	0	0	16	16351.122
{phi(TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16387.351	531.617	0	0	16	16355.345
{phi(g+ry1+reachALL) p(g+t+ry1+reach1+TL,TL^2)}	16396.275	540.541	0	0	19	16358.267
{phi(g+ry1+reach1) p(g+t+ry1+reach1+TL,TL^2)}	16399.379	543.645	0	0	19	16361.371
{phi(reach1) p(g+t+ry1+reach1+TL,TL^2)}	16399.498	543.764	0	0	17	16365.492
{phi(ry1+reach1) p(g+t+ry1+reach1+TL,TL^2)}	16401.223	545.489	0	0	18	16365.216
{phi(ry1+reachALL) p(g+t+ry1+reach1+TL,TL^2)}	16401.225	545.491	0	0	18	16365.218
{phi(reachALL) p(g+t+ry1+reach1+TL,TL^2)}	16461.357	605.623	0	0	17	16427.351
{phi(t+ry1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16612.493	756.759	0	0	19	16574.485
{phi(g+t+ry1) p(g+t+ry1+reach1+TL,TL^2)}	16635.292	779.558	0	0	19	16597.284
{phi(t+ry1) p(g+t+ry1+reach1+TL,TL^2)}	16637.383	781.649	0	0	18	16601.376
{phi(t+ry1+seas) p(g+t+ry1+reach1+TL,TL^2)}	16647.395	791.661	0	0	20	16607.386
{phi(g+t) p(g+t+ry1+reach1+TL,TL^2)}	16671.954	816.220	0	0	17	16637.948
{phi(t) p(g+t+ry1+reach1+TL,TL^2)}	16672.325	816.591	0	0	14	16644.321
{phi(ry1) p(g+t+ry1+reach1+TL,TL^2)}	16676.638	820.904	0	0	14	16648.634
{phi(g+ry1) p(g+t+ry1+reach1+TL,TL^2)}	16678.052	822.318	0	0	15	16648.047
{phi(g) p(g+t+ry1+reach1+TL,TL^2)}	16696.751	841.017	0	0	15	16666.746
{phi(.) p(g+t+ry1+reach1+TL,TL^2)}	16698.598	842.864	0	0	13	16672.594
{phi(g+t+ry1+seas+reachALL+TL,TL^2) p(.)}	16808.886	953.152	0	0	16	16776.880
{phi(g+ry1+TL,TL^2) p(g+t+ry1+reach1+TL,TL^2)}	16814.168	958.434	0	0	18	16778.161
{phi(g+ry1+seas) p(g+t+ry1+reach1+TL,TL^2)}	16867.072	1011.338	0	0	19	16829.064
{phi(.) p(.)}	18069.725	2213.991	0	0	2	18065.725

Appendix C. First-interval survival rate (ry1 phi) estimates and 95% confidence intervals for average-length (301.5 mm TL) razorback suckers reared by three methods and stocked into the Upper Colorado River Basin, Utah and Colorado, 2004–2007, averaging across each method's seasons and reaches of stocking.

interval	tank		pond		intensive	
2004–2005			0.20	(0.153–0.261)	0.27	(0.154–0.427)
2005–2006	0.04	(0.002–0.360)	0.06	(0.044–0.081)	0.09	(0.046–0.153)
2006–2007	0.03	(0.002–0.302)	0.04	(0.029–0.068)	0.06	(0.035–0.112)
2007–2008	0.04	(0.002–0.383)	0.06	(0.038–0.094)	0.09	(0.046–0.155)