Population Structure, Abundance and Recruitment of Colorado Pikeminnow of the Upper Colorado River, 1991–2015

Final Report

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LIST OF KEY WORDS

Colorado pikeminnow*, Ptychocheilus lucius,* Colorado River, mark-recapture abundance estimation, endangered Colorado River fishes.

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EXECUTIVE SUMMARY

Mark-recapture studies from 1991 through 2015 were used to assess population trends of Colorado pikeminnow *Ptychocheilus lucius* in the upper Colorado River. Five multi-year data collection efforts were made: 1991–1994, 1998–2000, 2003–2005, 2008–2010, and 2013–2015. Primary objectives included capturing and marking Colorado pikeminnow ≥ 250 mm in total length (TL) from throughout the study area, developing estimates of population abundance and survival rate and assessing trends in recruitment. Although results of the first four study periods have been provided in previous reports, we provide here a synthesis of some of those results with those from the most recent study period, 2013–2015.

The 178-mile-long study area was divided into two reaches: (1) the lower reach, extending from the confluence of the Colorado and Green rivers in Canyonlands National Park, Utah, upstream to Cottonwood Wash at the base of Westwater Canyon, Utah, and (2) the upper reach, extending from Westwater Wash at the top of Westwater Canyon, Utah, upstream to the Grand Valley Project Diversion Dam near Cameo, Colorado. The upper reach also included the lowermost 2.2 miles of the Gunnison River downstream of the Redlands Diversion Dam at Grand Junction, Colorado. The 12-mile-long Westwater Canyon, separating the 99-mile-long upper reach from the 112-mile-long lower reach, was excluded from study because few Colorado pikeminnow are thought to reside there and because it is difficult to sample. During the first two multi-year sampling periods, three passes were completed through the upper reach and two passes were completed through the lower reach. Backwater trammel netting was the primary means of sampling with shoreline boat electrofishing sampling supplementing the catch. In most cases, one two-person crew did all the sampling. Currently, four two-person crews worked concurrently: two in the upper reach; two in the lower reach with electrofishing sampling being the primary method of collecting Colorado pikeminnow. Most of the recent sampling was completed with electrofishing. Depending on the duration of runoff, three to five passes through each reach were completed each year. In all sampling periods, captured Colorado pikeminnow were measured, weighed, PIT-tagged and released.

For the 1991–2015 mark-recapture data, the Huggins estimator within the robust design multi-state data type of Program MARK was used to generate abundance and survival estimates. The Huggins estimator of population size was used to incorporate the individual covariate, total length, as a predictor of capture probability. Annual survival rates were estimated between primary occasions (years) in the robust design multi-state model. Covariates used to predict survival included year, reach, and fish length. Parameters were estimated for each reach separately and these estimates were combined to produce population-wide values. Due to a change in PIT tag and reader technology in 2004, a new capture history matrix was developed using only capture data from individuals tagged with the new tag type and included years 2004–2015.

Fifteen combined-reach annual abundance estimates and one earlier (1991) upper-reach estimate indicated the Colorado River population increased from 1991 through 2005. Combined-reach point estimates of individuals $\geq$ 450 mm TL increased from 440 in 1992 to 889 in 2005. However, abundance estimates significantly declined between 2005 and 2009 and remain significantly below the 2005 estimate. Probability of capture varied among years and reach. Overall annual survival rates (combined-reach estimates) for fish $\geq$ 500 mm TL appeared to decline over time from 88% (1991–1994) to 86% (1998–2000) to 80% (2003–2005). There was no fish length effect found using the recent data, and apparent survival rates were 76% in the lower reach and 87% in the upper reach for years 2008–2015.

Annual recruitment (number of fish 400–449 mm TL) appeared to exceed the estimated number of annual mortalities of fish $\geq$ 450 mm TL in eight of the 15 years for which estimates were available. The estimated net gain for the 15 years studied was 178 fish $\geq$ 450 mm TL. Because estimates were not available for years without sampling, total gain or loss for the 24-year period could not be estimated.

Precision of estimates affects the ability to detect change in population abundance over time. Precision of adult (>450 mm TL) abundance estimates as measured by the coefficient of variation (CV; smaller number indicates higher precision) was lowest during the first multi-year effort (mean CV of 24%), higher during the second, third, and fifth multi-year efforts (mean CVs of 14%, 15%, and 15% respectively), and highest in the fourth (2008–2010) period (mean CV of 12%).

Although the Colorado River population of Colorado pikeminnow remains self-sustaining, the recent decline in abundance is cause for concern. Estimated recruitment has been weak and not kept pace with adult mortality during some years. Mark-recapture studies of fish in large rivers are labor-intensive, and estimates of abundance and survival often have less-than-desirable levels of precision. They nevertheless appear to be the most reliable method for monitoring the status of Colorado pikeminnow populations.

INTRODUCTION

Colorado pikeminnow *Ptychocheilus lucius* once ranged throughout warm-water reaches of the Colorado River Basin, from the Wyoming border south to the Gulf of California. The species is currently restricted to upper basin reaches, upstream of Glen Canyon Dam, and is federally classified as an endangered species (USFWS 2000). The largest population occurs in the Green River sub-basin, and includes fish inhabiting the mainstem Green River, two primary tributaries, the White and Yampa rivers, and some smaller tributaries such as the Duchesne, Price and San Rafael rivers. Abundance in that sub-basin was estimated at 2,128 adults in 2013 (Bestgen et al. 2018). A Colorado pikeminnow population was also reestablished in the San Juan River. The San Juan River population of Colorado pikeminnow was essentially extirpated during the 1990s but has been augmented with hatchery-produced individuals (Ryden 2003). The mainstem Colorado River upstream of the Green River confluence (Figure 1) hosts the second largest wild population. The status and trends of that population are the focus of this report.

Estimating abundance of Colorado pikeminnow in the mainstem Colorado River sub-basin began in 1991. Results from an initial four-year, mark-recapture, field effort (1991–1994), were provided by Osmundson and Burnham (1998). These included annual abundance estimates and an estimate of annual adult survival rate averaged over the four-year period. A second field effort spanned 1998–2000, and abundance estimates were provided by Osmundson (2002). These studies also provided information on other important Colorado pikeminnow life history attributes including dispersal patterns (Osmundson et al. 1998), mean length-at-age, age-at-first reproduction, and sex ratio (Osmundson et al. 1997, Osmundson 2006). Results from a third and fourth multi-year, mark-recapture field effort conducted during 2003–2005 and 2008-2010 were reported by Osmundson and White (2009; 2014). Results from the most recent effort (2013–2015) are provided along with a synthesis of results for the entire 1991–2015 period.

Our goal was to provide annual abundance estimates of the Colorado River population of Colorado pikeminnow, with coefficients of variation of 20% or less. Such estimates, in conjunction with other population metrics, would then be used to assess population status and trends. Objectives included: 1) capturing and marking juvenile and adult Colorado pikeminnow (and opportunistically, bonytail (*Gila elegans*), humpback chub (*Gila cypha*), and razorback sucker (*Xyrauchen texanus*)), while making four to five sampling passes through the study area, 2) assessing trends in abundance and recruitment levels of Colorado pikeminnow, and 3) removing all non-native piscivorous fishes encountered while sampling.

METHODS

Study Area

Sampling was conducted throughout those portions of the upper mainstem Colorado River currently inhabited by Colorado pikeminnow (Figure 1). Colorado River locations are described herein as river miles (RM) from the Green River confluence (RM 0.0) as were mapped by Belknap and Belknap (1974). The study area was partitioned into two major reaches, lower (RM 0–112) and upper (RM 124–194). The 12-mile-long Westwater Canyon, separating the two reaches, was not sampled because of logistic difficulties and because past studies indicated low Colorado pikeminnow occurrence (Valdez et al. 1982).

In addition to the mainstem Colorado River, the upper reach study area also included the lowermost 2.2 miles of the Gunnison River downstream of the Redlands Diversion Dam. In 1996, Colorado pikeminnow gained access to the Gunnison River upstream of the dam following the completion of a fish ladder. Upstream dispersal past the diversion, blocked during the first study period (1991–1994), became possible prior to the start of the second study period (1998). All fish moving upstream through the ladder were first captured in a fish trap, sorted and identified before release. Tagged Colorado pikeminnow that moved upstream of the fish ladder were accounted for, and untagged individuals were tagged before release. Upstream movements through the ladder occurred primarily in July or August, either after the annual mark-recapture sampling was completed or during the last sampling effort of the year. Consequently, emigration from the study area did not violate the assumption of geographic closure for the within-year population estimates. Some of the individuals that used the ladder were later found using it a second or third time or were recaptured downstream of the dam in the lower Gunnison River or in the Colorado River, indicating they had passed down over the dam sometime after they first ascended it (Burdick 2001; Francis 2019a). Hence, use of the ladder did not necessarily mean an individual fish had been permanently removed from the study area. However, those that passed upstream and were never again detected downstream were assumed removed from the study area for survival estimate purposes. No attempt was made during this study to estimate the number of Colorado pikeminnow in the Gunnison River upstream of the dam.

Through 2005, the mainstem Colorado River study area extended from the Green River confluence upstream to Palisade, Colorado, where the Price Stubb Dam (RM 188.3), built in 1911, blocked further upstream fish movement. In early 2008, a fish ladder was constructed that allowed fish passage during low-water conditions. The study area was therefore extended 5.4 miles upstream to the base of the Grand Valley Project Diversion Dam (also-known-as Government Highline Diversion Dam; herein GVPDD) at RM 193.7, where a new fish ladder, equipped with a fish trap, allowed monitoring of fish moving up and out of the study area. Sampling in the 5.4-mile reach between the old Price Stubb Dam location and the GVPDD was conducted beginning in 2008.

Fish Capture and Handling

Capture methods during the 2013–2015 effort followed those of the earlier multi-year efforts, previously described in the aforementioned reports (Osmundson and Burnham 1998; Osmundson 2002; Osmundson and White 2009; 2014). Those procedures common to all five multi-year efforts are briefly described here along with a description of changes made to the sampling protocol in more recent years.

A combination of trammel-netting and electrofishing was used to capture both Colorado pikeminnow and razorback sucker ≥ 250 millimeters (mm) long during early-April to late-June. Trammel nets (1.8 meters [m] deep with a 2.5-centimeter- [cm] bar-mesh, inner panel and a 25-cm-bar-mesh, outer wall) of various lengths were used to capture fish from backwaters throughout the entire study area. Subadults and adults congregate in low-velocity, backwater habitats during spring when main-channel flow increases from snowmelt runoff (Osmundson and Kaeding 1989). During the first two study periods, use of electrofishing was largely restricted to capturing fish from shorelines in situations where backwaters were uncommon. Currently, shorelines throughout the study area are sampled with electrofishing equipment regardless of whether backwaters are present within the reach.

Fish were actively entrapped in nets by the ‘scare and snare’ method (Osmundson and Burnham 1998). One net was placed at the mouth of each backwater and, if the backwater was large, additional nets were set inside the backwater. The total number of nets set (1–7) increased with backwater size. A motorized aluminum jon boat used for net setting was then driven rapidly between the set nets in an effort to scare the fish toward the backwater mouth and thereby become entangled. Electrofishing does not occur in backwaters when trammel net sampling occurs in the backwater. When it was obvious that a Colorado pikeminnow hit a net and was entangled (tail or head seen above water at the top of a net), it was removed before other nets were set or checked for fish. As the nets were checked, captured Colorado pikeminnow were placed in a live well until all fish were removed from all nets. During the first two sampling periods, fish were anesthetized with MS-222 (tricane methanesulfonate), measured for maximum total length (TL: Anderson and Gutreuter 1983), weighed with an electronic balance (to the nearest gram) and electronically scanned for a passive integrated transponder (PIT) tag. If a PIT tag was not found, one was implanted in the body cavity using a hypodermic needle inserted 2–5 mm posterior to the base of the left pelvic fin. Fish were released after recovery from the anesthetic. During the latter three sampling periods, the same procedures were employed except fish were not anesthetized.

During the first two multi-year efforts, three sampling passes through the upper study reach and two passes through the lower study reach were made each spring, except in the lower reach in 1991, when only one pass was made. During these years, the first pass commenced in mid-April after runoff had begun and backwaters could be netted. This later changed to early April (see below). The goal was to complete sampling prior to the onset of spawning migrations. Colorado pikeminnow were targeted with sampling efforts, but other endangered fishes (bonytail, humpback chub, and razorback suckers) were also captured opportunistically. Piscivorous, nonnative green sunfish (*Lepomis cyanellus*), largemouth bass (*Micropterus salmoides*), northern pike (*Esox Lucius*), smallmouth bass (*Micropterus dolomieu*), and walleye (*Sander vitreus*) are also captured opportunistically and removed from the river. With each pass, every backwater deep enough to allow entry by boat (> 0.5 m) was netted. When electrofishing was employed, both shorelines were sampled in a downstream direction with a 5-m-long, hard-bottomed, electrofishing boat. Each boat had one netter stationed on the bow with a long-handled dip net. In reaches containing rapids, a 5-m-long, inflatable raft outfitted for electrofishing was used. Each craft was equipped with a Coffelt VVP-15 during the first two multi-year efforts. Either a VVP-15 or a Smith-Root GPP was used during the 2003–2005 and 2008–2010 efforts. Beginning in 2013 and consistent with Upper Colorado River Endangered Fish Recovery Program electrofishing guidelines, ETS electrofishing units were utilized (Martinez and Kolz 2018). All three electrofishing units produced pulsed DC.

During the two early multi-year efforts, capture data for portions of some passes were supplemented with capture records obtained from unrelated studies conducted by CPW, U.S. Fish and Wildlife Service (USFWS), and the Utah Division of Wildlife Resources (UDWR). Beginning in 2003, capture records were supplemented only with data from other USFWS-Grand Junction FWCO studies. Data from other studies were collected using similar boat-electrofishing methods.

Because the variance associated with the annual abundance estimates was considered high during the first two multi-year efforts, reducing variance by capturing and recapturing more fish per year became a goal beginning in 2003. To accomplish this, the number of passes per year and the sampling effort per pass were both increased. The initiation of sampling was moved up to early April prior to runoff so there would be sufficient time for additional passes. Because backwaters were not yet flooded, only electrofishing was employed during passes in early April.

Limited runoff in the upper Colorado River basin prevented adequate flooding of backwaters in the study area during 2003 and 2004; consequently, electrofishing shorelines replaced trammel netting as the primary capture technique during these years. No trammel netting was done in 2004. When conditions allowed, each daily sub-reach was sampled with one netting boat that moved from backwater to backwater and one electrofishing boat that sampled habitat on either shoreline, depending upon where the operator perceived the best Colorado pikeminnow habitat to be located. In contrast to the first two sampling periods, electrofishing was done throughout the upper and lower reaches during the latter three sampling periods. To sample the whole study area in a relatively short period, two crews worked in the upper reach while two other crews worked in the lower reach. Each pass generally took 10 days to complete in the upper reach and 12 days in the lower reach.

The goal during the latter three multi-year sampling periods was to complete four to five passes annually, however, the number of passes varied. Four passes were made through both reaches in 2003. In 2004, a rapid decline in water levels in June resulted in an early initiation of Colorado pikeminnow spawning activities, so sampling ceased after three passes. Because of a low rate of within-year recaptures that year, third-pass capture data in the upper reach were supplemented with post-spawning July capture data collected during an unrelated USFWS study (non-native fish removal). In 2005, five passes were completed in the lower reach and four in the upper reach. To provide a fifth pass for the upper reach, July capture data collected during the non-native fish removal project were again used. In 2008, 2009, and 2010, four passes were made in the lower reach and five in the upper reach. Data for the fifth pass in 2010 were again collected during the post-spawning, non-native fish removal project in July. Colorado pikeminnow captured at the Redlands fish ladder were also included in the fifth pass. In 2013, only three passes were completed on the lower reach. Data for the fifth pass on the upper reach in 2013 were again collected during the post-spawning, non-native fish removal project in July. In 2014 and 2015, four passes were completed on the lower reach and five passes were completed on the upper reach prior to July of each year.

Analyses

Survival rate and abundance estimation.

A capture history matrix was developed with each row representing a unique fish (identified by PIT-tag number) captured between 1991 and 2005, with columns representing sequential sampling passes. The length at capture and the reach the fish was captured in was entered in each column for each pass in which the fish was encountered. Rows were grouped by reach in which the fish was first encountered (initial captures in the lower-reach followed by initial upper-reach captures). Thus, the completed matrix, with new captures listed in chronological order, indicated not only the history of captures of each fish by primary (year) and secondary occasion (within-year pass), but also the capture length and reach through time. These data were then used as input to Program MARK (White and Burnham 1999). Colorado pikeminnow that were last detected moving upstream of the Redlands fish ladder were designated as ’removed’ and zeros were inputted in subsequent passes of the capture history matrix and therefore ignored in the likelihood calculation so that mortality rate would not be overestimated.

Beginning with the 2008–2010 analyses, we abandoned the old capture-history matrix and developed a new one. The reasons for this were as follows: starting in 2004, we began tagging with a newer 134 kilohertz (kHz) PIT tag, instead of the previously used 400 kHz tag. Through 2005, we checked for old 400 kHz PIT tags in captured Colorado pikeminnow. For those individuals found to contain an older 400 kHz tag, we re-tagged them with a new 134 kHz tag. So for two years, we had two PIT tag readers on each boat: one for the old 400 kHz tags and one for the new 134 kHz tags. Over time, the old PIT tag readers failed and the manufacturing company refused to repair them. During the first few years of PIT tagging (1991–1993), an early version of the older 400 kHz tags was used, and these could not be read by the new PIT tag readers. Hence, many early fish in our matrix could not be 'recaptured' in recent years, thereby biasing some aspects of model output. We needed to detect old 400 kHz tags in stocked razorback sucker (*Xyrauchen texanus*) that we encountered, so starting in 2008 the new PIT tag readers were programmed to detect both tag types while on one setting and technicians were instructed to leave that setting unchanged. The drawbacks to using this setting are that: 1) the ability to detect either tag type is reduced (i.e., lower reader sensitivity while in this mode), and 2) only the new 134 kHz tags (with the stronger signal) were often detected if both tag types were present in a fish (i.e., the old 400 kHz tag was not always detected).

Because of the uncertainty associated with reliably detecting the old 400 kHz tags with the new PIT tag readers, we developed a new matrix beginning with 2004 captures, the first year the new 134 khz tags and readers were used. Although abundance estimates were already developed for 2004 and 2005 from the earlier matrix, adding these primary periods to the new matrix had some benefits: when probability of capture (*p*) is low (0.1 or less), as is typical with Colorado pikeminnow captures, estimates of population size ($\hat{N}$) for a given year are improved when the matrix contains capture data for primary and secondary periods preceding the most recent years. Hence, variance associated with the estimate of $\hat{N}$ was reduced when capture data from 2004 and 2005 were added to the 2008–2010 capture-history matrix. Additionally, estimating survival rate for the interval between 2005 and 2008 was made possible by adding 2005 capture data to the matrix.

To use length as a covariate, lengths for each captured fish were needed for each year of the study. However, because individual fish were not captured in each sampling year, their lengths in years when not captured had to be estimated by interpolation or extrapolation. Of three models (von Bertalanffy, logistic, and Richards [1959]) fitted to the measured lengths during the earlier 1991–2005 analysis, the von Bertalanffy model provided the best fit based on the smallest mean squared error, so it was used to interpolate/extrapolate missing lengths both then and for the new analysis. For fish that were captured more than once within a year, the mean of the measured lengths was used for that year. To fit the model, a difference equation was assumed, following generally the procedures of White and Brisbin (1980):

$$L_{i+1} = (t_{i+1} - t_i)k(L_\infty - L_i) + L_i,$$

where L_i is the length at year i, t_i is the actual year of the observation, k is the von Bertalanffy growth coefficient, and L_∞ is the asymptotic length. To estimate the two parameters, the equation was implemented recursively, with $t_{i+1} - t_i = 1$. So, to predict a length for 1998 from a length in 1994, for example, the equation was first applied with the observed length from 1994 to predict a 1995 length. The predicted 1995 length was then used to predict a 1996 length, and this process repeated until the 1998 length was predicted. The model was thus used to produce individual covariate values of length for each year. Using these lengths, an input file for Program MARK was created.

The robust design multi-state data type was fit to the encounter histories with two states: lower and upper reaches. Primary occasions were years, and secondary occasions within years were sampling passes. Annual survival rates (*S*) were estimated between primary occasions in the robust design multi-state model, following Bestgen et al. (2007). Covariates used to predict survival in the earlier (1991–2005) analysis included year, reach and fish length, but only reach in the 2004–2015 analysis.

Population abundance estimates were generated with the Huggins (1989, 1991) estimator, with $p = c$ (i.e., initial capture probability each year was assumed equal to the recapture probability on subsequent passes with no change in capture probability as a result of capture within the year). The Huggins estimator was used because it allows inclusion of individual covariates, which we planned to incorporate. In a previous analysis, Osmundson and White (2009) considered models of p that included flow, water temperature, and number of boat days for each pass when modeling temporal variation in p within and between primary occasions. Because none of these models explained temporal variation in p then, they were not considered for the 2008–2010 or 2013-2015 analyses.

Estimates were constructed by using model averaging with model weights from the combined analyses to obtain estimates for four size classes of Colorado pikeminnow: ≥ 250 mm TL (essentially all sampled fish), 400–449 mm TL (Recovery Goal length criterion used to define fish about to recruit to adulthood; USFWS 2002), ≥ 450 mm TL (Recovery Goal length criterion used to define adults; USFWS 2002), and ≥ 500 mm TL (length criterion for adults assuming a minimum adult length of 476 mm for most males and 525 mm for most females; Osmundson 2006). Confidence intervals for $\hat{N}$ were computed using the lognormal transformation of the estimated number of animals never seen ($\hat{f}_0$), with the number of animals seen (M_{t+1}) added. The formulae for the lower and upper boundaries are LCI = $\hat{f}_0 / C + M_{t+1}$ and UCI = $\hat{f}_0 \times C + M_{t+1}$, where

$$C = \exp\left\{1.96 \times \sqrt{\log_e\left[1+\left(\frac{SE(\hat{N})}{\hat{f}_0}\right)^2\right]}\right\} .$$

Annual abundance was calculated for each of the two reaches, and these estimates were summed to provide annual population estimates for the entire study area. Variance around these summed estimates was calculated by the delta method (Seber 1982) with covariances included in the estimate. Coefficient of Variation (CV: 100 x SE/$\hat{N}$) was also calculated and used as a measure of estimate precision. An accepted precision standard is a CV of 20% or less (Pollock et al. 1990). To evaluate whether the population increased or decreased, we used the overlap or non-overlap of 95% confidence intervals as evidence of statistically significant differences among annual, combined-reach, abundance estimates (Schenker and Gentleman 2001).

Recovery Goal criteria for downlisting Colorado pikeminnow include the requirement that mean annual recruitment to the adult population balances or exceeds the number or rate of adult annual mortality (USFWS 2002); i.e., that the population is self-sustaining. To make this evaluation, length criteria were set forth in the Recovery Goal document defining adults as all individuals $\geq$ 450 mm TL and subadults about to recruit as all individuals 400–449 mm TL. We attempted to ascertain the frequency and magnitude of annual net gains and losses of individuals $\geq$ 450 mm TL by estimating annual abundance of individuals 400–449 mm TL and subtracting the estimated number of deaths $\hat{N}(1-\hat{S})$ of fish $\geq$ 450 mm TL (based on the survival rate estimated for the applicable three-year period).

In addition, trends in population abundance were assessed using a weighted regression technique, after Bestgen et al. (2010). To describe changes over time, regression relationships of abundance as a function of time were fitted that included intercept-only models as well as those with linear (T) and quadratic (T^2) terms. Using this technique, we analyzed trends in abundance for Colorado pikeminnow $\geq$ 450 mm TL for each reach and for the two reaches combined. Weighted regression uses estimates from the variance-covariance matrices produced from program MARK as weights for abundance estimates as a means to address the uncertainty (sampling covariances) around each point estimate. The weight of an individual estimate in the regression is inversely related to the estimate variance, e.g., more variable estimates get less weight, which can be assessed by the confidence limits. Akaike's Information Criterion (AIC_c) model selection (Akaike 1973) and weights were used to assess the level of support for each of the three competing models (intercept-only, linear, and quadratic). Model weights were proportions between 0 and 1, with weights of the three models summing to 1. The model with the greatest weight was interpreted as the one best describing the trend, and the greater the weight, the more support for that model. If the highest weight was given to the intercept-only model, it would indicate no substantial change in abundance over time (a relatively stable population); if highest weight was given to the linear model, the population likely increased or decreased in abundance over time in a consistent manner; if highest weight was given to the quadratic model, it would describe a population wherein an increase in abundance followed a decrease in abundance, or vice versa. For both the linear and quadratic models, directions in trends are indicated by negative (decreasing) and positive (increasing) terms. See Bestgen et al. (2010) for a more thorough description of the weighted regression technique.

Transition probabilities

The probability that a fish would move between the upper-reach and lower-reach study areas sometime between primary sampling periods can be estimated with the multi-state model and is termed a 'transition probability' (psi, ψ). Because transition probabilities were found to vary with fish size, we used a length of 500 mm TL as a standard to make among-year comparisons.

Catch-per-effort

Trends in catch rates using only results from years after the new electrofishing protocol was implemented (i.e., 2003–2005, 2008–2010, and 2013–2015) were compared. Although time of year (spring) was similar to earlier ISMP sampling, we used all areas sampled in calculating catch-per-unit-effort (CPUE) and not just subsets of the study area as was done during ISMP sampling. A sample was one day of boat electrofishing, typically on one shoreline. Annual sample sizes included all boats in all passes. Osmundson and White (2009) found comparisons of CPUE data collected prior to 2003 were not appropriate.

Mean number of fish per trammel net set was also used as another measure of catch rate. Trammel net catch rates from 1992–1994 and 1998–2000 were previously reported by Osmundson (2002) for Colorado pikeminnow as well as for other species of fish captured in the same nets. We provide here trammel net catch rates for years 2003–2005, 2008–2010, and 2013–2015 for Colorado pikeminnow. Both electrofishing and trammel net catch rate data was log-transformed as data were not normally distributed. Comparisons were made using Tukey's Honestly-Significant-Difference (HSD) Test ($P<0.05$;SYSTAT13).

Length frequency

Although abundance estimates and capture rates provide insight into intermediate-term population trends, high variance associated with these estimates limits understanding of short-term population dynamics. Examination of length-frequency histograms can be useful in interpreting transitions between reaches and providing information on recruitment history. Lengths of captured fish were partitioned into 10-mm categories and the number of captured fish falling into each category was converted to a frequency and graphed. For this study, aspects of length data were best viewed when fish were partitioned by capture reach. This was because Colorado pikeminnow age-classes (and therefore length-classes) were distributed throughout the study area differently (i.e., older and larger individuals occur predominately in upstream reaches and younger individuals in downstream reaches. Prior to presenting the recent length frequencies developed from Colorado pikeminnow captured in 2013–2015, we review those from earlier sampling efforts.

Temporal variation in length

Rather than gauge relative strength of a year-class from the number of larvae or young-of-the-year (YOY) present in the year of origin, we attempted to gauge strength by assessing the effect the cohort had on the size structure of the adult population after it recruited, some seven or more years after being produced (Osmundson and White 2009). A cohort was considered a ‘strong’ year-class if it resulted in a distinct decrease in median length of the adult population. Tracking average length of the adult population through time is similar to tracking average age. However, length is much easier to determine than age and, because the two variables are related, can be used as a surrogate index. The upper reach subpopulation consisted almost entirely of adults and was therefore a useful group to monitor to gauge the effect of a cohort on the adult population. We used the median length as an index for tracking changes in average Colorado pikeminnow size because the mean can be unduly influenced by the capture of a few large fish.

Relative year-class strength

In addition to total length, we used relative abundance at the late juvenile stage as a means to gauge strength of cohorts and estimate the frequency of weak, moderate, and strong recruitment year-classes. The frequency of strong year-classes is an influential factor in the future status of a population. As Colorado pikeminnow grow beyond age-5 it becomes progressively difficult to assign age to an individual based on its length. We used abundance at age-5 as a surrogate for recruitment strength with the assumption that many fish surviving to age-5 would also likely survive to become adults. Relative strength at age-5 was assessed by examining annual length frequency histograms of lower-reach-captured fish and comparing relative abundance of age-5 individuals among years. Individuals were considered age-5 if they were among a pulse of fish with lengths corresponding to this age. Although length varies among individuals, and mean length of a pulse or group of lengths varies among years due to variation in growing conditions in the preceding years, the mean of a discreet group of lengths can be used as a gauge to the group's age. Using scale aging, Osmundson et al. (1997) reported a mean length of 315 mm TL for age-4, 376 mm TL for age-5, and 424 mm TL for age-6 Colorado pikeminnow (see Appendix Table I). We assumed individuals in an identified group of fish were age-5 if their group's mean length was closer to the reported mean length (see Appendix Table I) of age-5 fish than to the reported means of age-4 or age-six fish. We also used the length range of age-5 fish reported in the scale-aging study (356-453 mm) as a guide. After the 10 mm increment length frequency histogram was examined, the sorted actual lengths were examined for break points and for calculating a mean for the group. When no obvious break point could be discerned among year-classes from the sorted lengths, larger individual lengths were not included if they were outside the expected age-5 length range or if adding them increased the mean to where it became closer to that reported for age-6 fish. We assigned each year-class to one of three qualitative strength categories based on the relative contribution that age-5 individuals made to the total number of lengths sampled (Weak: 0-15%; Moderately strong: 16-50%; Strong: 51-100%). For years when no sampling occurred, frequency of age-5 fish could not be examined. In those cases, we estimated year-class strength at age-5 based on relative abundance of age-4 fish in the preceding sampled year or age-6 or age-7 fish in a subsequent sampled year.

Inter-system movements

Movement of marked Colorado pikeminnow between the Colorado and Green River systems was assessed through inspection of the Species Tagging, Research and Monitoring System (STReaMS 12/16/2019) database maintained by the Upper Colorado River Endangered Fish Recovery Program and the San Juan River Recovery Program. Captures of Colorado pikeminnow by field crews and detections at PIT tag antennas were included in the analysis of inter-system movements. An inter-system movement was identified when an individual fish captured in one system was later recaptured in the other system. Movement of Colorado pikeminnow between the Colorado River system (Colorado and Gunnison rivers) and the Green River system (Green, San Rafael, White, Price, Duchesne, Little Snake and Yampa rivers) was previously documented by Osmundson and White (2009) with capture-recapture data through 2010. Here, we update our summarization of such movements using additional data collected from 2013 through 2015.

Razorback Sucker Parameter Estimates

Data collection for the razorback sucker abundance estimate occurred simultaneously with sampling focused on Colorado pikeminnow. As stocking location and timing varied by year and to avoid a “first year in the river effect” (Zelasko et al. 2018), the matrix only included a razorback sucker if the fish had been in the wild for at least one over-winter period since being stocked. Model selection procedures and covariates included in the models were similar to those described for Colorado pikeminnow parameter estimates for c, S, $\hat{N}$, and ψ.

RESULTS

Fish Captures

There were 472 unique Colorado pikeminnow captured during the recent 2013–2015 study period. The new capture-history matrix, extending back to 2004 and ending with 2015, included 1,083 unique individuals. The prior matrix (1991–2005) included 1,258 unique fish. The new matrix consisted of 31 lower-reach passes and 37 upper-reach passes. Numbers of captures per pass and reach ranged from 10 to 60 (Table 1).

Model Selection

Parameters for the von Bertalanffy growth curve were estimated, with an asymptotic size of 830 mm TL (Table 2). These values were used to predict fish lengths for unobserved fish in the robust-design multi-state model. For the 2004-2015 dataset, the minimum AIC_c model {S(reach) ψ(reach*TL) p(reach*year*pass) DM} included a reach effect on survival (*S*), but no time effect on *S* (Table 3). Survival is assumed constant across those years, but different in the two reaches. Transition probability (ψ) between the two reaches (movements from lower to upper reach and from upper to lower reach) included a length effect. Initial capture probabilities varied by reach, year and pass.

Capture Probability

When fish length was held constant (500 mm TL), capture probabilities were highly variable between reaches and within and among reaches, years and passes (Figure 2; Appendix Table II). Capture probabilities were especially low in 1992 in the lower reach, and in 2003 and 2004 in both the lower and upper reaches. In the upper reach, the mean probability of capture during 1991–2000 (0.094; $n = 21$) significantly differed ($P < 0.0001$) from 2003–2010 (0.055; $n = 27$), but there was no difference in mean capture probability between years prior to 2000 and after 2010.

Survival Rate

The top model for the 2004–2015 capture data did not include a length effect on survival, unlike the top model for 1991–2005. Additionally, there was no year effect supported by the top model for any time period. Because of this, annual survival estimates were the same for all years after 2005. Annual survival rate was significantly higher in the upper reach than in the lower reach (Figure 3). In the upper reach, estimates of annual survival of Colorado pikeminnow for each multi-year sampling period were similar, ranging from 89.0% (1991–1994) to 85.9% (2003–2005) (Figure 4). In the lower reach, estimates of annual survival ranged from 81.5% (1991-1994) to 76.1% (2013-2015) These earlier estimates were for Colorado pikeminnow ≥ 500 mm TL (the top model included a length effect). The most recent estimate, for 2008–2015, was 86.9% and included all fish in the capture-history matrix (≥ 250 mm TL). No significant differences in annual survival rate estimates among the multi-year periods were found for either the upper or lower reach.

Population Size

Annual abundance estimates for the four length groups of Colorado pikeminnow in the two reaches, and in the two reaches combined, are provided in Appendix Tables III–VI. As previously noted, no summed estimate for both reaches is provided for 1991 because no lower-reach estimate was available for that year. Abundance of 400–449 mm-long Colorado pikeminnow (those about to recruit) is reported in the Population Replacement section below.

For Colorado pikeminnow ≥ 250 mm TL, abundance estimates for the lower reach ranged from 332 (2009) to 1,192 (2003), and for the upper reach, from 196 (2014) to 416 (2005); summed estimates ranged from 582 (2010) to 1,516 (2003). For individuals ≥ 450 mm TL, abundance estimates ranged from 156 (2013) to 492 (1993) in the lower reach and 176 (2013) to 410 (2005) in the upper reach; summed estimates ranged from 332 (2013) to 897 (2005). For fish ≥ 500 mm TL, estimates ranged from 75 (1992) to 315 (2005) in the lower reach and from 175 (1993) to 376 (2008) in the upper reach; summed estimates ranged from 277 (2014) to 668 (2005). Based on non-overlap of 95% confidence intervals, only a few abundance estimates were significantly different from one another (Figure 4). Specific estimates by reach, TL and year are available in Appendices III-VI.

Precision of annual estimates was generally higher (lower CVs) for the upper reach than for the lower reach for each of the three major length categories (Appendix Tables III-V), though not for the 400-449 mm length group. During the most recent three-year effort

(2013–2015), the mean CV for Colorado pikeminnow >450 mm TL in the combined reaches was 15.5%. However, the best single year for this length group in the combined reaches was 2005, with a CV of 10.6%.

From an earlier analysis by Osmundson and White (2009), a variance components trend analysis indicated fish $\geq$ 450 mm TL significantly increased from 1992 to 2005. Maximum likelihood population estimates indicated a positive trend over time (slope: 12.26/year; SE: 4.12) that significantly differed from zero (Wald chi-square: 8.8; $P = 0.003$), as was the case for fish $\geq$ 500 mm TL (slope: 10.29/year; SE: 3.36; Wald chi-square: 9.4; $P = 0.002$). Slopes reported were estimated increases of fish per year. However, for fish $\geq$ 450 mm TL, point estimates indicated this upward trend did not continue into the recent study period so the variance components module of MARK was not performed here. Declines from the 2005 abundance estimates for fish $\geq$ 450 mm TL occurred in both the upper and lower reaches (Figure 5).

Population Replacement

Abundance estimates of Colorado pikeminnow 400–449 mm TL were used to ascertain whether recruitment balanced adult mortality. Abundance estimates and length frequency histograms from 2013–2015 indicated Colorado pikeminnow 400–449 mm TL (Recovery Goals criterion for fish about to recruit; USFWS 2002) were rare in the upper reach during these years (Figure 6). Abundance estimates for 400–449 mm TL Colorado pikeminnow in the upper reach ranged from 22 individuals in 2013 to 4 in 2015. In the lower reach, the three recent annual estimates ranged from 76 to 176 individuals. Because this length group is a small subset of the total population in most years, captures and recaptures were very limited, resulting in wide confidence intervals around $\hat{N}$ in most years with the exception of 2013-2015, large standard errors, and CVs greater than the recommended 20% (Appendix Table VI). Despite this imprecision, the combined-reach abundance estimates, along with mortality rate estimates, provide a means to assess whether recruitment equaled or exceeded adult mortality. For years 1992–1994, we used an adult mortality rate of 12.2%; for years 1998–2000, 14.7%; for years 2003–2005, 16.2%. Mortality rates were calculated by subtracting the estimated survival rate (see parameter estimate subheading for more information) from one. For years 2005–2015, we applied the lower-reach mortality rate

(23.8%) to the lower reach abundance estimate and the upper-reach mortality rate (13.1%) to the upper-reach abundance estimate. Results indicated an estimated loss of 37 fish ≥ 450 mm TL from apparent mortality in the lower reach during 2013 and a gain of 176 fish from recruitment, for a net gain of 139 fish. In the upper reach, there was an estimated loss of 23 fish and gain of 22 fish in 2013. In 2014, there was an estimated net gain of 5 fish ≥ 450 mm TL in the lower reach (mortality loss of 71; recruitment gain of 76) and a net loss of 16 fish in the upper reach (mortality loss of 24; recruitment gain of 8). In 2015, there was an estimated net gain of 33 fish ≥ 450 mm TL (52 fish loss from mortality; 85 fish gained from recruitment) in the lower reach and an estimated net loss of 24 fish in the upper reach (mortality loss of 27; recruitment gain of 3). During the most recent study period for both reaches combined, there were estimated net gains of 138 fish in 2013 and 10 fish in 2015 and a net loss of 10 fish in 2014. Of the 15 years studied, there were estimated gains in eight of the years, and losses in the other seven years (Figure 7). Gains ranged from 1 to 183 individuals per year; losses, from 10 to 141 individuals per year. The estimated net gain for the 15 years studied was 178 fish ≥ 450 mm TL. Because estimates were not available for years not sampled, total gain or loss for the 24-year period could not be estimated.

Transition Probabilities

Most between-reach movements by Colorado pikeminnow in the Colorado River have been in an upstream direction, i.e., from the lower to the upper reach. Since 1992, we documented 60 such movements and 10 movements from the upper to the lower reach. Unless a fish was captured in one reach in one year and recaptured in the other reach the following year, the year in which the movement was made or the approximate size the fish was when it moved could not be identified.

From 2005 to 2015, the annual probability of a lower-reach, 500-mm-long fish moving to the upper reach was 7%. For lower-reach Colorado pikeminnow, there was a fairly high probability of movement to the upper reach between 1992 and 1993 (24%) and between 1993 and 1994 (23%). After 1994, there was a three-year hiatus in sampling and so transition probability could only be estimated for the entire period 1994 to 1998. During this interval, there was a 59% probability of movement to the upper reach. Assuming these movements were spread equally over these years, the average annual probability was 20% (Table 5). However, much of the movement may have occurred early in the four-year interval because from 1998 to 1999 probability of movement to the upper reach had dropped to 0% and was low during 1999 to 2000 (5%). Transition probability was 0% during the non-sampling interval between 2000 and 2003, and only 6% from 2003 to 2004.

For upper-reach Colorado pikeminnow, there was a 0% probability of movement to the lower reach in all years from 1991 to 1999. From 1999 to 2000 there was a 16% transition probability. During the subsequent non-sampling interval between 2000 and 2003, transition probability was 25%, or an annual average of 9%. Annual average transition probability in the upper reach moving to the lower reach for a 500 mm TL fish was 7% for years 2005-2015.

When the top model (minimum AICc) used for generating survival and abundance estimates from the 1991–2005 capture matrix was used for assessing the relationship between length and transition probability, the resulting relationship was not supported by empirical evidence. The model indicated that the smallest Colorado pikeminnow had the greatest probability of moving from the lower to the upper reach and this probability declined with increased length. However, length frequency histograms of Colorado pikeminnow captured from the upper reach (see Length Frequency section) indicated there were essentially no fish in the upper reach smaller than about 400 mm TL. In addition, of 14 cases in which the recapture in the upper reach occurred one year after initial capture in the lower reach, the smallest individual when captured in the lower reach (before having moved) was 402 mm TL, suggesting that few smaller individuals made the lower-to-upper reach transition.

Two additional post hoc models were developed to provide a more biologically realistic relation between length and transition, or at least one more consistent with the empirical data (not shown; see Osmundson and White 2009). Because of the small number of fish that made transitions and the four additional parameters in the quadratic spline compared to the minimum AICc model, this quadratic spline model {*S*(reach+length^2) ψ (reach*t+reach*length^2 + quad spline) *p*(reach*primary*t+length^2)} did not have a lower AICc than the top model and thus was not used for estimating abundance or survival.

Because the new 2004–2015 matrix had a more limited data set, with few transitions during the period, we were unable to update the earlier (1991–2005) spline model. The original results for 2004–2005 were retained (Table 5) because it was calculated with the larger and therefore more data-rich matrix. The new matrix did not indicate a time effect so probabilities for lower-to-upper transitions for periods from 2005 to 2015 were identical (7%).

Electrofishing Catch-per-Effort

Mean electrofishing catch rates (Colorado pikeminnow ≥ 250 mm TL/hr of electrofishing) per pass were fairly consistent in the upper reach during the years of 2013–2015, with no significant differences between passes within a year or between years (Figure 8). In the lower reach, catch rate was more variable. In 2014, the first pass catch rate in the lower reach was significantly higher than the electrofishing catch rate from the third and fourth passes. Confidence intervals overlap for other within year passes in 2013 and 2015. There was no consistent trend of catch rates either increasing or decreasing within years.

Mean annual catch rates were significantly lower in 2013 than in 2008 in the upper reach (Figure 9). In the lower reach, mean annual catch rate was significantly higher in 2015 that in 2008 and 2009 (Figure 9). In the two reaches combined, no significant differences were found between catch rates across years (Figure 9).

River-wide electrofishing catch rates for all Colorado pikeminnow ≥ 250 mm TL were not significantly different than for catch rates of Colorado pikeminnow ≥ 450 mm TL (Figure 10). In years 2008 and 2009, the catch rates of Colorado pikeminnow ≥ 250 mm TL and catch rates of Colorado pikeminnow ≥ 450 mm TL were very similar, indicating that captures of fish 250–449 mm TL made up a relatively small proportion of the overall catch.

Trammel-Net Catch-Per-Effort

The number of trammel nets set varied by reach and year. In both reaches, no trammel net sampling was attempted in 2004. The number of nets set per year ranged from a low of 38 (1991) to a high of 291 (2009) in the lower reach. In the upper reach, the number of nets set per year ranged from a low of 51 (2005) to a high of 145 (1998).

Mean catch rates during 1991, 2003, 2008–2010 and 2013–2015 were significantly lower than those during 1998–2000 in the upper reach (Figure 11). Mean catch rates in 2010 and 2015 were significantly lower than in all years during the 1990's in the upper reach. In the upper reach, where individuals were almost exclusively ≥ 450 mm TL, catch rates generally increased from 1991 through 2000, but then dropped off. The catch rate in 1998 was significantly higher than in 1991 and 1992, and catch rates in 1999 and 2000 were significantly higher than in 1991. Catch rates in 2003 and all subsequent years were significantly lower than in 1998.

Length Frequency

In the upper reach, increased frequencies of young adults signal transition events (dispersal from the lower to upper reaches) and increased frequencies of large adults signal an aging population. Length frequencies in the lower reach are useful in estimating relative strength of cohorts soon to recruit (see section on recruitment indices below).

In the upper reach, almost all fish captured during 2008–2010 were ≥ 500 mm TL (Figure 12). The only exceptions were two fish in 2009 that were 490–499 mm TL. There was therefore little evidence of young individuals having recently migrated to the upper reach from the lower reach. Those that did migrate upstream, may have done so at larger sizes.

In the upper reach, the majority of Colorado pikeminnow captured during 2013–2015 were ≥ 500 mm TL (Figure 13). While the majority of Colorado pikeminnow captured were > 500 mm TL, more Colorado pikeminnow < 500 mm TL were captured during 2013–2015 sampling than were captured during the previous (2008–2010) sampling period.

There were more large adults captured in the lower reach during 2003–2005 and 2008–2010 than in the early 1990s and the 2013–2015 sampling period. During 1991–1994 (Figure 14), individuals > 650 mm TL made up 0–2% of the sample; during 1998–2000 (Figure 15), 0–8%. During 2003–2005 (Figure 16), large adults made up 5–12% of the sample; during 2008–2010 (Figure 17), 8–10%. Large adults > 650 mm TL made up 4.9% of the captures in the lower reach during the 2013–2015 study period (Figure 18).

In the upper reach, percentages of individuals > 650 mm TL were similar during the first two sampling periods (1991–1994: 25–35%; 1998–2000: 24–36%), but markedly increased during the 2003–2005 period (47–66%) and remained high during 2008–2010 (46–57%). Growth of the strong and moderately-strong year-classes produced during 1985–1987 likely contributed to the increased percentage of larger fish. During 2013–2015, the percentage of fish > 650 mm TL in the upper reach was 39–61%. The percentage of adults captured that were large (≥ 800 mm TL) varied among years but generally increased by the end of the study period: during 1991–1994, 0–14%; during 1998–2000, 3–5%; during 2003–2005, 8–10%; during 2008–2010, 11–17%; during 2013–2015, 15–19%.

Recruitment Indices

A decline in the median length of adults in the upper reach was first observed in the early 1990s (Figure 19), and resulted from an infusion of young recruits (1986 year-class) to the adult population, i.e., the number of small adults entering the population was great enough to offset the effect that growth of older adults had on the median length. By 1998, the median length had increased and was essentially back to where it had been in 1991, suggesting that the upstream dispersal of small adults had dropped off during the intervening (non-sampled) years of 1995–1997. This increase in median length continued through 2000 indicating fish growth had a greater effect on median length than did addition of young adults.

The median length of upper-reach fish in 2003 (633 mm TL) was higher than in 2000, and by 2004, was considerably higher (693 mm TL), continuing the trend seen in 1998–2000 (Figure 19). However, this trend reversed in 2005 when substantial numbers of sub-adults and young adults were captured in the upper reach (presumably the 1998 year-class) causing the median length to again decline. This is supported by the transition rate results which indicated the highest level of lower-to-upper reach movement occurred between 2004 and 2005 (Table 5). Although there is a gap in the records (no sampling in 2006 and 2007), this decline in median length evidently continued through 2008. The trend then reversed and median length steadily increased through 2014, suggesting that upstream movement of young adults to the upper reach had tapered off. In 2015, median length in the upper reach decline again, suggesting movement of small Colorado pikeminnow into the upper reach.

In 1991, fish estimated to be age-5 made up 76% of the sample captured from the lower reach (Figure 14; Table 6). The 1986 year-class therefore ranked out as the strongest recorded during the study period. Relative abundance of age-5 fish in 1992 (19% of sample) suggested 1987 was a year-class of moderate strength. The 1988 year-class appeared to be very weak based on the relative rarity of fish estimated to be age-5 in 1993 (6% of sample). The 1989 year-class was a little stronger at age-5 (an estimated 12% of sample) than the 1988 year-class but it too ranked out as weak.

After a three-year hiatus, it was difficult to identify year-classes within the 1998, lower-reach, length-frequency histogram (Figure 15). There was, however, a distinct group of fish with lengths (520–609 mm TL) consistent with what we might expect from fish hatched from 1985 to 1987 (age-11 through age-13). If so, this group would represent the remainder of the large pulse of fish first observed in 1991. For fish younger than this, there was a small gap that likely reflected the very weak year-class of 1988 noted above. Following this gap was a continuous block of fish ranging in length from 334 to 500 mm TL. There were no distinct break points within this group suggesting a series of weak-to-moderately strong year-classes estimated to be age-4 through age-7 (1991 through 1994 year-classes). We assigned a group of these to age-5 and the 1993 year-class ranked out as one of moderate strength (17% of sample). Rarity of age-5 fish in the 1999 sample (8%) suggested 1994 was a relatively weak year-class. In 2000, there were only three fish captured (6% of sample) that may have been age-5. Their mean length was outside the range of what we would expect for age-5 fish (412 mm TL), but the sample size was very low. In any case, 1995 was clearly a weak year-class.

When sampling began in the lower reach in 2003, a large proportion (64%) of the captured fish had lengths corresponding to those expected of age-5 fish (Figure 16). Their high relative abundance indicated that 1998 was a strong year-class. The 2004 histogram indicated a relatively small number of age-5 fish in the captured sample (10%) such that the 1999 year-class ranked out as weak. Finally, in 2005 there was a new, distinct group with lengths corresponding to age-5 fish, i.e., the 2000 year-class. Their relative abundance in the sample (17%) suggested a year-class of moderate strength.

In the lower reach in 2008, there were very few captures of Colorado pikeminnow < 400 mm TL, suggesting the lack of a recent strong or even moderately-strong year-class (Figure 17). The paucity of age-5 fish in 2008 (7% of sample) strongly suggested that 2003 was a weak year-class. In 2009, there were only four fish captured (5% of sample) with lengths corresponding to age-5, suggesting 2004 was also a very weak year-class. However, in 2009 a group of young Colorado pikeminnow 240–309 mm TL (mean length = 271 mm) were captured (estimated as age-3 or age-4). By 2010, the length range of this group had increased to 320–409 mm TL (mean = 367 mm), the size expected of age-5 fish (2005 year-class). These accounted for 27% of the lower-reach sample (Figure 16) and 2005 therefore ranked as a year-class of moderate strength.

Strong year-classes of Colorado pikeminnow estimated as age-5 were observed in the lower reach during 2013 and 2015 (spawned in 2008 and 2010). In 2013, 51 Colorado pikeminnow (estimated as age-5) with a mean TL of 413 mm (range 371–450 mm) were captured in the lower reach. In 2015, 45 Colorado pikeminnow (estimated as age-5) with a mean TL of 393 mm (range 365–435 mm) were also captured. Only seven Colorado pikeminnow estimated to be age-5 were captured in 2014 suggesting the 2009 year-class was weak.

In 1995, the first non-sampling year, relative abundance of age-5 fish could not be assessed; however, low numbers of age-4 fish captured in the previous year (1994) suggested that 1990 was likely a weak year-class. The 1991 and 1992 year-classes were the most difficult to assess. Based on the relative abundance of what were estimated to be age-6 and age-7 fish in the 1998 histogram, and abundance of age-7 fish in the 1999 histogram, the 1991 and 1992 year-classes were judged to have been of moderate strength. No sampling was done in 2001 and 2002, but the almost complete absence of captured fish in 2000 with lengths expected of age-4 fish suggested that 1996 was a very weak year-class. In 2003, there was a very low number of fish 436–514 mm TL suggesting that age-6, age-7, and age-8 fish were scarce, and year-classes 1997, 1996 and 1995 were all weak. No sampling was done in 2006 and 2007, but a scarcity of age-4 fish in 2005 suggested 2001 was likely a weak year-class. The small number of fish 375–476 mm TL captured in 2008 (age-6 and age-7), indicated that both 2001 and 2002 year-classes were fairly weak. Based on low numbers of captures of age-4 fish in 2010 and age-6 fish in 2013, both 2006 and 2007 appear to be weak year-classes of Colorado pikeminnow.

In total, our best estimates of year-class strength, based on decreases in median length of upper-reach adults and relative abundance of age-5 fish captured from the lower reach, suggested there were 15 weak, seven moderate, and only three strong year-classes produced between 1986 and 2010 (Table 6).

Movements Into and Out of the Green River System

Limited use of PIT tags to mark Colorado pikeminnow began in the Colorado River in 1990 and was fully adopted as the standard tagging method throughout the upper basin in 1991. Between 1990 and 2015, there was a total of 17,973 encounters reported in the upper-basin of Colorado pikeminnow that were PIT-tagged at the time of encounter or previously (Table 7; STReaMS 12/16/2019). These included 4,495 encounters in the Colorado River system and 13,478 encounters in the Green River system. To discern whether a fish made an inter-system movement, at least two encounters of a fish must be made.

From 1991 to 2015, there were 77 documented inter-system movements. Twenty-one of these events were one year apart; another 19 such events were two years apart. Five of the encounter occurred in the same year as the preceding encounter (one to six months apart). The greatest elapsed time between encounters was nine years. Some of the fish were sub- or young adults when the movement occurred, but most were $\geq$ 500 mm TL when last encountered before moving to the other river system. The stationary PIT tag antenna on the Green River canal detected 15 of the 77 fish, despite this PIT tag antenna being a relatively recent (2013) installation. One of the 77 fish was also detected in 2013, 2014 and 2015 on the stationary White River PIT tag antenna.

Many of these fish moved relatively long distances. Eight fish moved over 400 miles (644 km) between encounters. Four fish moved from the Colorado River to the Green River and then back to the Colorado River. One fish was encountered in Lake Powell in 2014. All fish that moved to the Colorado River system were previously caught in the Green River mainstem (not in a tributary). Colorado pikeminnow that moved from the Colorado River to the Green River Basin, were encountered in the Duchesne (1 fish), White (1 fish) and Yampa (7 fish) Rivers.

Fifty-one individuals encountered in the Colorado River system moved to the Green River system and 25 fish encountered in the Green River system moved to the Colorado River system. Six fish moved to the other basin but later returned to the basin in which they were originally encountered. Four of these fish moved from the Colorado to the Green River basin and later returned; two moved from the Green to the Colorado River system and later returned.

Razorback Sucker Parameter Estimate

Razorback sucker abundance was calculated with capture data collected during this project (Figure 20, Appendix VII). Abundance estimates range from 5,035 to 8,078 razorback suckers for the entire study area during the recent study period (2013–2015) and are significantly higher than the estimate from 2008, but confidence intervals overlap for other years. Estimates from the upper reach range from 2,251 to 3,684 razorback suckers for years 2013–2015, but confidence intervals overlap for all years. Estimates from the lower reach for years 2013–2015 range from 2,784 to 4,393 razorbacks and are significantly higher than the 2008 estimate.

In 2013, 41 untagged, suspected wild-produced razorback suckers less than 250 mm TL were captured during sampling for this project. Only one of the 41 suspected razorback suckers captured in 2013 has been recaptured and it was identified as a razorback/flannelmouth sucker hybrid. While suspected wild-produced razorback suckers were captured in 2013 in our study are, the abundance estimates are most likely comprised of stocked razorback sucker, and the increasing trend is the result of continued stocking of the species, not natural recruitment. The CV for the combined estimates was below 15% for all years during the recent study period, indicating an acceptable level of precision (Appendix VII).

Survival estimates for razorback sucker were 69.8% in the lower reach and 59.4% in the upper reach. Confidence intervals associated with the survival estimates overlap, indicating no difference. The top model included a reach and TL effect on apparent survival

(Table 8). As there was no year effect, razorback sucker survival estimates were constant across both study periods (2008–2010 and 2013–2015). As a length effect was included in the top model for survival, the survival estimates are for razorback suckers of 400 mm TL. The top two models also included a reach effect on transition probability and a reach, pass and year effect on probability of capture.

DISCUSSION

Model Selection

Model selection results using the new 2004–2015 capture-history matrix differed from those produced earlier when the larger 1991–2005 matrix was used. Previously, the best model that explained the data (model with the minimum AIC_c) included reach and fish total length effects on survival (Osmundson and White 2009 and 2014). The new best model included a reach effect but no fish length effect. Also, the earlier best model had transitions (lower to upper reach and upper to lower reach fish movements) as time- and length-specific. Like the previous model updated in 2010, the new 'best' model, though length specific, was not time specific (probability of movement did not vary by year). The earlier best model also indicated that initial capture probabilities (*p*) were reach-, length-, and time-specific (for both primary and secondary periods); however, the new best model indicated initial capture probabilities, though reach- and time-specific, were not length-specific. We would expect how these parameters (survival, movement, and probability of initial capture) vary, whether by year, reach, or fish length, would be relatively constant traits of the population. The fact that the new, smaller capture matrix, with fewer years and fewer fish than the earlier matrix, did not support a length effect for survival nor for probability of capture, or a time effect for transitions, suggests that these changes may be a function of the limited data set rather than a change in the biological nature of the fish. It makes intuitive sense that survival rate would be related to fish size and that probability of movement would be year-specific. As additional annual capture data accumulate in the future, we may see the best model again include these effects.

Capture Probability

The decline in capture probability from the first half (1991–1998) of the long-term study period to the second half (2003–2015) is noteworthy. The reduction appeared to occur abruptly between year 2000 and 2003. A decreasing trend in probability of capture has also been found during monitoring of the Green River Colorado pikeminnow population (Bestgen et al. 2018). Surprisingly, this was when our effort per pass was increased from one boat crew to two. Although capture efforts emphasized electrofishing, trammel-netting was still done when conditions allowed, just as before. Probability of capture was expected to increase. Trammel net catch rate also declined during the latter half (2003–2015) of the study period in the upper reach. This had earlier been a very effective means to capture Colorado pikeminnow. As mentioned before, the decline in trammel-net catch rate was not correlated with a commensurate decline in the population as measured by abundance point estimates. This suggests that the effectiveness of trammel netting actually declined and may be one reason behind the reduction in capture probability. Two large warm backwater sites in the upper reach where we earlier routinely caught Colorado pikeminnow with trammel nets were physically modified around this time transforming them into side channels during runoff. The elimination of these habitats may have played some role in reducing trammel-net catch rates. Another possibility is that these long-lived fish became wary of capture and handling and learned to avoid backwaters where they were vulnerable to our nets. This explanation is unlikely, however, because of the abruptness of the decline in trammel-net catch rates. We currently have no recommendations regarding how we might increase capture probabilities.

Survival Rate

The primary results regarding survival were that survival rate was significantly lower in the lower reach than in the upper reach during the most recent period (2013–2015). Lower-reach survival-rate estimates appeared lower than in the upper reach in the previous study periods also but differences then were not statistically significant. Although the estimated lower- and upper-reach rates for the recent period were included in Figure 3 to illustrate long-term trends in survival rate, the comparison with earlier estimates was not entirely valid. The model that produced the recent estimates did not include a fish length effect and so estimates therefore reflected the survival rate of all captured fish ($\geq$ 250 mm TL) and were not specific, as before, to that of adult fish ($\geq$ 500 mm TL). This would have little effect on the upper-reach survival rate estimate because almost all fish there were $\geq$ 500 mm TL anyway. However, for the lower reach, the inclusion of smaller fish (250–499 mm TL), may have lowered the estimate because earlier analyses indicated lower survival rate in smaller Colorado pikeminnow. Thus, the lower-reach estimate may have been somewhat higher if a length effect had been indicated by the current top model and only adult fish included in the survival estimate.

Our recent estimates of annual survival of 86.9% in the upper reach and 76.1% in the lower reach can be compared with the results of Bestgen et al. (2007, 2010, and 2018), because those investigators also included all sizes of fish in their analyses. They reported survival rate for the Green River population as 65% during 2000–2003, 80% during 2006–2008, and 72% during 2011–2013. However, their top model in both instances did not include a reach effect and therefore our observation of lower survival rate in lower versus upper reaches of the Colorado River study area could not be corroborated in the neighboring Green River system.

Although survival estimates take into account movements from lower to upper reaches (and vice versa), they do not take into account movements out of the study area. Evidence that marked fish leave the Colorado River study area and move to the Green River system may, in part, explain why survival rates in the lower reach are consistently lower than in the upper reach. As explained by Bestgen et al. (2007), estimates of survival are really estimates of ‘apparent’ survival because survival = 1- mortality and the estimation model, based entirely on recapture probabilities, does not differentiate between actual mortality and emigration from the study area. Hence, emigration is a subset of estimated or ‘apparent’ mortality. Some part of the difference in ‘apparent’ survival between the lower and upper reaches is likely due to unequal emigration rates.

Population Size

The degree to which population abundance fluctuates depends on the size range of fish being considered. Because recruitment comes in infrequent pulses, some years have many more young fish than other years. Therefore, the difference in combined-reach, annual, abundance point estimates for all fish ≥ 250 mm TL ranged from 582 (2010) to 1,517 (2003), with the highest year being 2.6 times greater than the lowest year. For fish ≥ 450 mm TL, abundance estimates ranged from 332 (2013) to 897 (2005). Although strong year-classes eventually result in increased adult numbers, there is a damping effect from mortality that prevents large short-term fluctuations in adult numbers. For individuals ≥ 500 mm TL, combined-reach estimates ranged from 295 (2013) to 668 (2005) with the highest year 2.25 times greater than the lowest year. The lag effect of growth also influences when a given size-class reaches its greatest numbers following a strong year-class. That is, for fish ≥ 250 mm TL, the year with the greatest abundance was 2003; for fish ≥ 450 mm TL and ≥ 500 mm TL, it was 2005.

Combined-reach abundance estimates of Colorado pikeminnow ≥ 450 mm TL (Recovery Goal adult length criterion, USFWS 2002) exhibited a positive and significant slope during the first 13 years of the study period (1992–2005), increasing by 102%. This increase in abundance was followed by a 52% decline through study years 2013-2015, returning to numbers similar to those in 1992 in only five years. Abundance of adult Colorado pikeminnow remains low compared to the abundance estimate in 2005. Although adult abundance does not fluctuate as dramatically as abundance when younger ages are included, population abundance can decline fairly rapidly in the absence of strong year-classes. Bestgen et al. (2007) documented a similar, significant decline in adult Colorado pikeminnow abundance in the Green River system when estimates dropped by 48% between 2000 and 2003 and the decline has continued in 2006–2008 (Bestgen et al. 2010) and 2011–2013 (Bestgen et al. 2018). In that instance, evidence suggested it was the combined result of low recruitment and a significant reduction in adult survival. The recent decline in the Colorado River population is likely attributable primarily to low recruitment as survival estimates have remained relatively constant. However, a possible decline in adult survival rate in the lower reach, though not as extreme as in the Green River, may have also contributed to this decline.

Population Replacement

Estimates of annual population replacement indicated a gradual increase in the population of Colorado pikeminnow ≥ 450 mm TL in the Colorado River study area between

1992 and 2005 (Osmundson and White 2009). When the estimated number of deaths of fish ≥ 450 mm TL was subtracted from abundance estimates of Colorado pikeminnow 400–449 mm TL in the concurrent year, a gain was indicated in six of the nine years (1992–2005) for which we had data, with a summed net gain of 332 individuals ≥ 450 mm TL. Currently, with the six most recent years added, nine of 15 years had an estimated gain in individuals and six years had an estimated loss. Accordingly, the summed net gain since 1992 has decreased to an estimated 178 fish ≥ 450 mm TL.

The weighted regression analysis indicated that the annual combined-reach population estimates were best described by the intercept-only model, suggesting the population was stable over the first 19 years of the study period (1992–2010, 12 abundance estimates; Osmundson and White 2014). One advantage of the weighted regression analysis is that it takes into account the variance around the abundance point estimates and weights each estimate accordingly. In contrast, trend analyses that add recruit-sized fish and subtract mortalities rely entirely on point estimates of abundance and survival with no regard to the size of the variance about the estimates, lending a great deal of uncertainty to the results. Fortuitously here, results of the two methods were in general agreement.

Although the analyses indicated a stable population for the series of years examined, we must add a cautionary note. Abundance estimates of individuals ≥ 450 mm TL during the most recent years indicated a significant decline: the combined-reach point estimates of 897 in 2005 dropped to 332 in 2013, a 63% reduction in eight years. In the absence of recruitment, an annual mortality rate of only 12% (survival rate of 88%) can account for such a reduction. Although these calculations are based on point estimates, the weighted regression analysis did lend support to the notion that at least the upper reach sub-population decreased in abundance following an earlier increase (quadratic model; Osmundson and White 2014). Whether a decline has continued during the past two years in which sampling did not occur (2016 and 2017) or whether the population has since been ‘rescued’ by a significant recruitment event will determine whether the trend can continue to be characterized as ‘stable.’

Transition Probability

Transition probability estimates are useful in determining whether dispersal to the upper reach is a continual, steady process or whether it occurs in pulses. Also, the timing and magnitude of movement in both directions helps shed light on within-reach population dynamics.

High upstream transition probabilities noted in the early- to mid-1990s and from 2004 to 2005 are consistent with observations of pulses of young fish detected in the lower reach in both 1991 and in 2003. As these fish grew, many moved upstream. An increase in the upper-reach abundance point estimate in 1998 compared to that in 1994 is consistent with the positive net upstream transition probabilities during that interval. Upstream movements of this first pulse of young fish had evidently almost ceased by 1998 ($\psi^{LU} = 0.0$), perhaps indicating the pool of fish inclined to move had become depleted. Additionally, the decline in upper-reach point estimates from 1998 through 2004 was consistent with the zero, low, and negative net upstream probabilities estimated for those years. Finally, a notable increase in upper-reach abundance in 2005 was consistent with the high net upstream transition probability (30%) estimated for the 2004–2005 period. Although these increases and decreases in annual abundance point estimates were not statistically significant, they did fit what we might expect given the net transition probabilities.

Transition probability calculations benefit greatly from long-term capture histories. Output from the top model using the earlier, larger capture history matrix indicated a length effect (sub- and young adults were more likely to move than older adults) and a time effect (probability of movement between reaches varied by year; Osmundson and White 2009). Using the recent 2004–2015 matrix, no time effect was detected and sub- and young adult Colorado pikeminnow were uncommon until the last few years covered by the current matrix. As data from additional years of sampling are added to the current matrix, we may again see length or time effect on transition probability as we again have sub-and young adult Colorado pikeminnow in the Colorado River.

Electrofishing Catch-per-Effort

In the past, ISMP used annual electrofishing catch rates as a means to discern trends in Colorado pikeminnow population abundance (USFWS 1987). Although abundance itself could not be determined from catch rates, the assumption was that increases and decreases in catch rates reflected increases and decreases in abundance, thereby providing an index to abundance trends. However, for rates of capture to be proportional to abundance in a consistent manner, probability of capture must be fairly uniform across years. From recent mark-recapture analyses (Bestgen et al. 2007, 2010, 2018; Osmundson and White 2009, 2014), high variability in annual capture probability appears to be the norm, violating one of the key assumptions of catch-per-effort trend analyses. Because capture probability at time of sampling is estimated in mark-recapture studies and is taken into account when calculating abundance, estimates so derived should be considered more reliable for discerning population trends than catch-rate results.

Catch rates can provide something of a consistency check for trends indicated by annual abundance estimates. Osmundson and White (2014) superimposed mean annual electrofishing catch rates of Colorado pikeminnow over point estimates of abundance for the years 2003–2005 and 2008–2010 and found fairly good agreement in the overall trend for individuals $\geq$ 450 mm TL. The exception was year 2003, when catch rates were substantially lower than what might have been predicted from the abundance estimates. Colorado pikeminnow had the lowest probabilities of capture in 2003 than in any other year studied, and this may help explain the observed discrepancy in mean electrofishing catch rate and the abundance point estimate that year. The even greater disparity between catch rates and abundance estimates in 2003 for fish $\geq$ 250 mm TL might in part be explained by the relatively low probability of capture for the smaller size classes of fish (see Osmundson and White 2009: Figure 2). Hence, catch rates would appear lower than expected in years when there is a high number of young fish in the population as was the case in 2003 and 2004. Also, confidence intervals for population estimates were relatively wide in 2003, especially for fish $\geq$ 250 mm TL, and may also help explain the disparity between abundance point estimates and catch rates in that year, i.e., real abundance may have been lower than that indicated by the point estimate.

Because probability of capture in our studies is a function of both trammel-netting and electrofishing success, it is difficult to tell how much of the annual variation in $\hat{p}$ is attributable just to variation in electrofishing success. However, investigators in the Green River system, who have relied almost exclusively on electrofishing for mark-recapture sampling, have also found high among-year variability in capture probability (Bestgen et al. 2007, 2010). Despite the discrepancy noted for 2003, the trend in electrofishing catch rates generally supported the trend displayed by annual abundance point estimates for Colorado pikeminnow $\geq$ 450 mm TL: abundance increased from 2003 to 2005 and then declined from 2005 to 2010. Catch rates, for Colorado pikeminnow $\geq$ 250 mm, from the most recent study period (2013–2015) not significantly different than catch rates from 2010. Omitting earlier ISMP electrofishing catch rates and restricting our comparisons with abundance estimates to only those years in which equipment and protocol was consistent improved congruence between the two trend indices over earlier such comparisons (see Osmundson 2002).

Trammel-Net Catch-Per-Effort

Trends in annual trammel-net catch rates appeared to have little relation to trends in annual abundance estimates. Trammel-netting was so successful in the early years of the study (1991–2000) that it was used almost exclusively to capture Colorado pikeminnow for mark-recapture purposes. Use of backwaters, flooded canyon mouths, and flooded gravel pit ponds by Colorado pikeminnow during spring runoff may, in part, be more determined by hydrologic conditions during the sampling period than by the relative abundance of Colorado pikeminnow in the system at a particular time. At a minimum, water needs to be high enough to flood such habitats before they can be used. In addition, before flooded habitats attract Colorado pikeminnow, they may need to be warmer than the main channel, provide better feeding opportunities, or perhaps the main channel needs to reach relatively high velocities before backwaters are sought as shelter. Certainly, during large flow years, more flooded backwater habitat is available. However, this provides an unsatisfactory explanation for the trend in trammel net catch rates during the study period.

Catch rates in the lower reach significantly declined during the study period (1991–2010) and remained low through 2015, yet there was no corresponding decline in water volume during spring runoff during the same period. In the upper reach, annual trammel-net catch rates progressively increased during the first sampling period (1991–1994) as might be expected, corresponding to higher numbers of Colorado pikeminnow migrating there from the lower reach. However, the trammel-net catch rate was significantly lower in 2005, the year of highest adult abundance, than in 1998. Runoff conditions were similar during these years (peak flow at the USGS 09163500 CO/UT Stateline gauge in 1998 was 26,100 cfs; in 2005, 31,000 cfs; April-June water volume in 1998 was 2.88 billion m^3; in 2005, 2.93 billion m^3).

Skill in capturing Colorado pikeminnow with trammel nets may have increased during the first several years of monitoring. In the upper reach, one investigator was a trammel-netting crew member consistently from 1991 through 2000. Beginning in 2003, this person began working predominately in the lower reach and upper-reach trammel netting was subsequently conducted by various seasonal technicians. Hence, experience level may have played some role in the decline in catch rates in the upper reach after year 2000. However, this would not explain the decline in catch rates in the lower reach given that the experienced investigator was a consistent trammel-net crew member throughout the study period there.

A contributing factor in the decline of trammel net catch rates in the upper reach after year 2000 includes the loss of two key trammel net sites: the Walker State Wildlife Area ponds and Island Backwater. These two sites were physically altered to reduce high selenium concentrations in the water and biota by flushing the sites with river water (Osmundons and White 2014). The loss of these two prime trammel-netting sites, that had yielded 27% of upper-reach captures prior to 2001, likely contributed to later declines in annual, upper-reach, trammel-net catch rates.

Length Frequency and Relative Year-class Strength

Length-frequencies of captured Colorado pikeminnow were primarily useful in identifying strong and weak year-classes. As previously emphasized, the frequency of strong year-classes is perhaps the single most influential factor determining the status of this population. Clues that allow identification of strong year-classes aid our understanding of population dynamics. For small populations, such as Colorado pikeminnow in the Colorado River, judging the strength of a given year-class is somewhat subjective and relative to that of cohorts of other years. Length frequencies are used here in two ways: 1) as an index of the strength of a given cohort when it first appears in electrofishing and trammel-netting surveys (by the relative abundance of age-5 fish), and 2) how large a 'rescue' effect the cohort later has on the population (i.e., whether it results in a noticeable decrease in the median length of the adult population).

Over the 25-year, 1991–2015 period, three clear, strong, age-5 cohorts appeared in lower-reach samples: the first was the 1986 year-class (perhaps 1985–1987 combined classes); the second, the 1998 year-class. The third strong year-classes occurred in 2008. . Although high catch rates of YOY Colorado pikeminnow in fall seine surveys may portend strong year-classes, in the Colorado River, they are not always reliable indicators of strong recruitment later (see section below). By the time individuals of this species are age-5, they are presumably more immune to environmental factors that affect survival of early life stages. Relative abundance of age-5 individuals observed in length frequencies is probably a fairly reliable indicator of the strength of later recruitment to the adult population and dispersal to the upper reach.

Tracking average length of adults in the upper reach provided a secondary means of evaluating the relative strength of recruitment through time. A constant median length from year to year would be expected if recruitment and adult mortality were consistently balanced through time. However, as length-frequency data from the lower reach indicates, Colorado pikeminnow recruitment often comes in pulses, with only some years producing strong year-classes. The upper-reach, sub-population of adult Colorado pikeminnow experienced three declines in median length: the first from 1991 through 1994, resulting from an infusion of young adults from the strong year-class of 1986; the second, from 2004 through 2008, resulting from an infusion of young adults from the strong year-class of 1998 and the third in 2015 from the strong 2008 and moderate 2010 year-class. The general trend in the upper reach from 1998 to 2014, has been that of a steadily aging population, despite the temporary reversal in median length from the one strong year-class (1998) which slowed the aging trend. As this report only included data up to 2015, the effect of the moderate 2010 year-class on the upper reach has not been completely assessed. Tracking median length over time provides a bigger, longer-term view of the population and the relative impact of a given cohort. A possible gauge of whether a cohort can be considered a ‘strong’ year-class might be whether it is capable of temporarily reversing the aging trend (decreasing the median length) of the adult population.

Our qualitative estimates of relative abundance of age-5 fish in 15 annual length-frequency distributions (and age-4 and age-6 in seven others) suggests there were three strong year-classes produced during the 20-year period of 1986–2010. These three years, along with seven year-classes of moderate strength between 1986 and 2000, together fueled a significant increase in the adult population from 1992 through 2005. This was despite eight of the 15 years (53%) having relatively weak year-classes. However, length-frequency data suggests that after year 2000, there were four contiguous weak year-classes (2001–2004) followed by one year-class of moderate strength (2005). The adult population subsequently declined in abundance from 2005 through 2013.

Despite twelve years elapsing between the first and second strong year-classes, the adult population significantly increased during the first part of the study. The first strong year-class had a very large positive impact on the population, lowering the median length in the upper reach. Then, by 1998, median length began to increase. The population was temporarily 'rescued' when the year-class originating in 1998 began to recruit and the upper-reach median length again declined in 2005. This might suggest that a strong year-class every 12 years may be sufficient to maintain the population. However, in the more recent part of the study, the adult population significantly declined even though strong year-classes were lacking for only seven years. Although speculative, an explanation might include: 1) the first strong year-class (1986) was exceptionally strong and the second strong year-class (1998), while clearly helpful, did not have the strength and therefore lasting effect that the first did; 2) during the 12 intervening years between the first and second strong year-classes there were also four moderately-strong year-classes, whereas in the seven years following the second strong year-class there were only two year-classes of moderate strength. Hence, the question of how frequent 'strong' year-classes must be to maintain a stable or increasing adult population may not have a straight-forward answer. Rather, it may depend on the relative strength of the 'strong' year-class and by how much the intervening years also contribute to recruitment.

Relative Abundance of YOY and Later Strength of Recruitment

A Colorado pikeminnow year-class is strong at age-5 or when recruiting to the adult population because YOY were produced in high numbers in the year of origin and/or because survival during the juvenile phase was especially high. An understanding of how environmental factors affect production of YOY and survival of juveniles (and ultimately recruitment) is required before managers can devise effective strategies aimed at increasing the size of the Colorado River population. This can be done by tracking cohorts and identifying when significant declines in relative abundance occur. Research identifying environmental factors that are negatively affecting YOY or juvenile Colorado pikeminnow survival has not been attempted in the Colorado River, but has occurred in the Green River (Bestgen and Hill 2016).

Because the upper Colorado River is in the temperate zone, fish experience large seasonal changes in their environment, and each season brings its own unique set of pressures. By recurring annually, these pressures are predictable enough that a species can adapt a life strategy to cope with and even thrive under variable conditions. However, the magnitude of the pressures varies by year depending on current and antecedent weather conditions (largely driven by snowpack), adding a level of unpredictability to the environment. The long life span of Colorado pikeminnow allows for years of high and years of low reproductive success and years of high and years of low juvenile survival. Over time, successful recruitment years will make up for unsuccessful ones. High fecundity and long-life are traits that assure population persistence for populations that may experience extended periods of low recruitment success (Tyus 1986, Osmundson 2006). Colorado pikeminnow populations can thereby fluctuate in abundance over the short term while remaining stable over the long term. However, when successful years of recruitment do not keep pace with unsuccessful ones for a prolonged period, stability is lost, the population declines, and there is a danger of extirpation.

Two factors make it difficult to track abundance of a cohort through time: 1) movements of fish among habitats, and 2) the limitations of gear in capturing the fish at different stages of development. Colorado pikeminnow can be captured in backwater nursery habitat with seines during their first year of life. Standardized, YOY sampling in fall (late September-early October) provides an index of relative abundance at this early life stage. Young-of-year can again be found in these habitats the following spring prior to snowmelt runoff. However, many of these fish seemingly disperse to other habitats during or after runoff and are generally not found in appreciable numbers at age-1 when backwaters are again sampled for YOY the following fall (Breen et al 2011). Although small Colorado pikeminnow are sometimes captured with electrofishing or trammel-netting (when fine-mesh nets are used), they are generally not caught in appreciable numbers until about age-5.

Osmundson and White (2009) found that probability of capture varied by fish length and that fish < 480 mm TL were under-represented in a sample of captured fish from the lower reach, and probability of capturing an individual 250 mm TL was half that of one 480 mm TL. Hence, after YOY enter their first winter at 20–65 mm TL, they are generally not seen again until they become susceptible to sampling gear designed to capture larger fish. There is therefore about a four-year period during which mortality factors can act upon a cohort after the strength of the cohort is assessed during the first fall. Because mortality rate cannot currently be measured during this stage, mortality factors cannot be identified or assessed.

In general, fish are most vulnerable to environmental conditions when they are young and small. Because age-0 Colorado pikeminnow can be found in backwaters immediately following their first winter, the ISMP was expanded for nine years (1988–1996) to include spring sampling of backwaters so that comparisons could be made between YOY catch rates in fall with those the following spring. This was done as a means to assess the impact of first-year over-winter mortality. Results from the lower Green River were presented by Valdez and Cowdell (1999) and the lower Colorado River by McAda and Ryel (1999). In both cases, annual, over-winter survival (as measured by differences in CPUE) was highly variable, with rates of 23-100% in the Green River (mean of 48%) and 7-100% in the Colorado River (mean of 49%). Survival rates were less than 50% in five of nine cases in the Colorado River and six of nine cases in the Green River. However, McAda and Ryel (1999) suggested that mortality over the six months from early October to late March was probably no greater than mortality during the preceding summer and early fall, i.e., winter was not necessarily a particularly harsh period to survive. Whether fish actually died in backwaters over winter, moved to un-sampled habitats, or were displaced downriver and out of the study area (perhaps to the Lake Powell inflow), can only be surmised. Valdez and Cowdell (1999) found that CPUE declined significantly more, on average, in shallow backwaters than in deep ones when data from five years were pooled. They hypothesized that spring flow spikes from low elevation snowmelt (prior to spring sampling) may have displaced young Colorado pikeminnow from shallow backwaters sending them downstream to Lake Powell, whereas those overwintering in deeper backwaters (> 120 cm) were less likely to be displaced. In contrast, over-winter downstream movements of marked YOY Colorado pikeminnow further upstream in the middle Green River, documented by Haines and Modde (1996), indicated very limited downstream dispersal over winter. Despite the remaining uncertainties regarding the fate of over-wintering age-0 Colorado pikeminnow and related causes of mortality, it is clear that survival rates during the first six months following annual fall YOY sampling are highly variable. Thus, it should come as no surprise that survival rates to age-5, some four years later, would also be highly variable, and that catch rate of YOY in fall would not be a very reliable predictor of later year-class strength in the Colorado River.

Both Valdez and Cowdell (1999) and McAda and Ryel (1999) found significant correlation between CPUE of YOY in fall with CPUE the following spring. Though puzzling at first, given the high annual variation in survival, it makes sense that if CPUE is low in fall it will also be low in spring and unless an abundant cohort has relatively low over-winter survival, CPUE should still be high in spring relative to other year-classes. Looked at in this way, we might expect relative YOY abundance in fall to have some predictive power regarding later year-class strength despite the high variability of survival rates over the first winter. This, however, assumes that the most important sources of mortality occur prior to March in the first year of life, an assumption that probably should not be made given the results we provide here.

Osmundson and White (2014) compared long-term data from annual YOY sampling with length frequencies of Colorado pikeminnow collected by electrofishing and trammel netting five years later and found relative abundance of age-0 fish in fall to be a poor predictor of year-class strength at age-5 and presumably of later recruitment. The most abundant year-class (1996) of those studied by McAda and Ryel was later weak by the time it reached age-5. Additionally, the 1994 year-class remained weak through age-5 despite the relatively large initial size of individuals. Finally, as previously noted, the 1998 year-class began weak in terms of YOY relative abundance, but later (at age-5) became the strongest year-class in 12 years.

Inconsistency in relative cohort strength between age-0 and age-5 in roughly 40% of the 20 years suggests that mortality factors after fall of the first year often determine later recruitment levels. Certainly, over-winter mortality contributes to this. McAda and Ryel (1999) found what may have been size-dependent mortality in one of the nine winters studied: there was only 7% over-winter survival the year when fall YOY Colorado pikeminnow were significantly smaller than average (mean = 20.5 mm TL). They also documented over-winter longitudinal shifts in age-0 Colorado pikeminnow distribution with fall and spring distributions differing significantly in eight of nine years. This lends support to the aforementioned hypothesis of Valdez and Cowdell (1999) regarding early spring flow spikes that may overtop sand-bar-formed shallow backwaters and send age-0 fish downstream. Building on these findings, along with observations that additional mortality may be significant in some years following the first fall and early spring, we suggest that spring runoff in May and June may displace many more young Colorado pikeminnow downstream and out of the study area before they have completed their first year. In years of moderate to high spring runoff, most within-channel, sandbar-formed backwaters are submerged on the rising limb of the hydrograph and even deep backwaters that serve as refuges for young Colorado pikeminnow during winter and early spring are washed out. Although zero-velocity habitats exist along vegetated shorelines during runoff, there may nonetheless be a downstream shift in distribution of juveniles during runoff that could be substantial in some years. The relatively close proximity of the primary nursery habitat in the Colorado River (RM 20–50; Breen et al. 2011) to the Lake Powell inflow makes downstream shifts in distribution particularly worrisome because of the high densities of predacious sport fish that reside there (Persons and Bulkley 1982). At full pool, the inflow is approximately 14 miles downstream of the Green River confluence (34 miles downstream of the lower end of primary Colorado River nursery area). By August 2013, recent low runoff conditions had caused the Lake Powell inflow to recede some 39 miles downstream of the former full-pool inflow site. Increasing the distance between the nursery area and the lake inflow might benefit survival of young Colorado pikeminnow displaced downstream.

Unlike sandbar-formed, in-channel backwaters, flooded canyon mouths are stable, zero-velocity refuges during runoff that get deeper and warmer as runoff progresses and may provide critical holding and nursery habitat for early life stages of Colorado pikeminnow. Availability of these sites varies annually depending on river stage and sediment dynamics. Many are blocked in some years when silt bars form at the eddy-mouth interface (D. Osmundson, personal observation). Suitability of these sites as nursery habitat might also vary annually depending on depth and duration of inundation. Presumably, as juveniles enter their second and third year of life their increased size confers a greater ability to move against the current, select beneficial habitats and avoid downstream displacement.

Assumptions and Uncertainties

The robust design multi-state model employed here that produced separate annual abundance estimates for the two study reaches assumes demographic closure within each reach during the annual sampling period. This assumption appears to have largely been met. The Colorado River study area was closed to emigration at its upstream end (RM 188) by the Price-Stubb Diversion Dam through 2007. With passage provided in early 2008, upstream movement beyond RM 194 (the Grand Valley Project Diversion Dam) was monitored at a fish ladder and trap. Similarly, movement out of the mainstem Colorado River and up the Gunnison River was monitored at the fish ladder and trap at the Redlands Diversion Dam, 2.2 miles upstream of the Gunnison-Colorado river confluence. However, there were three exceptions to closure worth noting here: one entailed between-reach movements, the second is movements to and from the Green River system, and the third is fish moving into the unsampled Dolores River.

Of the 60 documented movements between reaches, two occurred during an annual sampling period: one in 2004 and one in 2005. In both cases, the first capture was in the lower reach and the second in the upper reach. In both cases, the second capture was at the Redlands fish ladder trap in the Gunnison River after the estimated spawning period. As mentioned earlier, third-pass data in 2004 were supplemented with captures made during July after the standard April-June sampling was over. Similarly in 2005, fifth-pass data for the upper reach consisted entirely of captures made during a smallmouth bass removal project in July. Hence, the assumption of closure within reaches appears to have been violated only during these two times and these violations occurred only when the standard sampling period was extended into or beyond the spawning period.

The effects on our abundance and survival estimates from Green River Colorado pikeminnow having entered our study area and from our marked individuals having left our study area when they moved into the Green River, are difficult to assess because the actual number immigrating and emigrating could not be estimated. For annual abundance estimation, the effects are probably negligible because immigration and emigration are only relevant if they occur during the annual sampling period. Of the 54 inter-system movements we documented over a 20-year period by Osmundson and White 2014, only one was known to have occurred during an annual sampling period. Based on the absence of documented movements between the upper and lower reaches of the Colorado River study area during April-June periods, it is reasonable to assume that inter-system movements might similarly occur mostly during times of the year other than the April-June period.

Survival estimates, on the other hand, are assessed over years rather than over months and would therefore be affected by movements that occur outside the annual sampling period. Because survival is estimated from capture histories of marked fish, such estimates would be unaffected by new unmarked fish having entered our study area from the Green River. However, the model cannot differentiate between mortality and emigration, so if marked Colorado River individuals left the study area during a survival estimation interval, the survival estimate would be biased low. There were 51 marked fish that we know emigrated from our study area to the Green River over a 25-year period (about two per year), so we might assume the resulting bias to our survival estimates was very low; however, we do not know the level of non-detection in the Green River. Biologically, the effects on the Colorado River population of emigration and mortality are the same. Because both result in losses of fish, our inability to tease the sources of loss apart is perhaps not that critical.

Unlike estimates of survival, which include emigration as part of mortality, our estimates of recruitment, based on abundance estimates of individuals 400–449 mm TL, would not include immigrants from the Green River if the individuals that immigrated fell outside of the 400–449 mm length-class. Of the 21 Green River Colorado pikeminnow that we know entered and, we presume, stayed in the Colorado River, at least 16 were larger than 450 mm TL when they immigrated. We can therefore conclude that our estimates of annual additions to the adult population are biased low to some unknown degree.

Other assumptions inherent in our mark-recapture methods, such as the susceptibility of all individuals to capture, minimal loss of marks (PIT tags), similarity of capture and recapture probabilities, and others, were well covered by Bestgen et al. (2007). The rationale provided by those authors for how such assumptions were met can be applied here because field methodologies and many of the analyses used by them and us were similar or identical.

For assessing year-class strength, using relative abundance of age-5 fish had its shortcomings. The incomplete record from the 2–3 year gap between multi-year sampling efforts made some year-classes difficult to assess because relative abundance had to be estimated at age-4 or age-6 rather than at age-5. No scale aging was done after 1992, and year-classes could only be assigned based on length ranges and mean length of groups of fish detected within length frequency histograms. Among-year variation in growing conditions (water temperatures, food availability) may result in fish lengths that don’t match the predicted average for a particular age-class. Also, the overlap in lengths among adjacent year-classes can make it difficult to assign a year of origin to some individuals in a group of fish of a given length. Hence, judging year-class strength from length-frequency histograms is a less-than-exact science and the qualitative results that we present should be viewed as best estimates only. To improve future assessments of year-class strength, a more reliable means to age juveniles when they are in the 325-450 mm length range is needed.

Inter-System Movements

Conclusions regarding movement between the two river systems (Green and Colorado) are difficult to make from capture-recapture data because comparisons do not take into account unknown differences in sampling effort or relevant detection parameters in each river system (i.e., relative percentages of each population sampled each year, relative percentages of each population that were tagged, relative survival rates of tagged fish, etc.). The stationary PIT tag antenna installed at the Green River canal in 2013 detected 15 Colorado pikeminnow that moved to the Green River from the Colorado River, even though the reader had only recently been installed. Prior to the recent study period, similar numbers of Colorado pikeminnow had been encountered moving between the sub-basins, but with the large number of detections at the Green River canal antenna, it appears that fish moving from the Colorado sub-basin to the Green River sub-basin are more likely to be encountered than fish moving from the Green to the Colorado.

The two sub-basins are treated as separate populations for the purposes of monitoring the species status relative to recovery goals, and the level of connectivity between the two systems (i.e., inter-system fish movement) is relevant to our understanding of demographics and gene flow. The level of exchange of individuals between the two groups affects whether the groups function as biologically separate populations. Aspects of this topic were previously discussed in detail by Osmundson and White (2009, 2014). Continued monitoring of inter-system movements of Colorado pikeminnow will be vital to estimating population parameters relative to recovery goals.

Fish Ladders

Although wild Colorado pikeminnow are captured ascending the Gunnison River at the Redlands Dam ladder (Burdick 2001, Francis 2019a), few have apparently remained upstream of the dam. Between 1996 and 2016, 180 captures of Colorado pikeminnow were made at the Redlands Dam ladder. During 12 electrofishing trips in recent years (two annual trips from 2011-2016) from Delta to Redlands Diversion Dam, all Colorado pikeminnow captures above Redlands Dam have occurred within one month of the fish being moved above Redlands Dam (Francis 2019a) .

Upstream movements past the diversion dams on the Colorado River have not resulted in Colorado pikeminnow persisting above the former movement barriers. During 2009 and 2010, one wild Colorado pikeminnow was captured in the reach between the Price Stubb fish ladder and the GVPDD. Three additional Colorado pikeminnow were captured at the more upstream GVPDD fish ladder since operation began in 2005 (Francis 2019b). This indicates low motivation on the part of Colorado pikeminnow for additional upstream dispersal, either because they are wary of using the ladder or because habitat suitability declines beyond this point (see Osmundson 2011 for a discussion of upstream temperature suitability).

To date, fish passage above movement barriers has largely failed to populate upstream reaches. Prospects for recovery of the Colorado River population would be enhanced if the river's major tributary, the Gunnison River, could be repopulated. An extension of range into a tributary would ensure survival of a group of adults in the event the core population in the Colorado mainstem was significantly reduced by a short-term catastrophe such as a chemical spill. The reasons that Colorado pikeminnow do not remain upstream of fish passage structures are unknown, but actions that promote increased recruitment in the Colorado River and improved habitat conditions in the Gunnison River are needed to address threats and to insure long-term persistence of this important population.

Impact of Nonnative Species

Northern pike, smallmouth bass and walleye all pose a serious threat to the recovery of native species (Martinez 2015). Northern pike, while rare in the portion of the Colorado River occupied by Colorado pikeminnow, are both a potential predator and competitor of

Colorado pikeminnow. Smallmouth bass, common throughout the upper reach of our study area, are also a competitor and pose a predatory threat to YOY and small juvenile Colorado pikeminnow. Prior to 2010, walleye were rare in the study area, but are now common within the lower reach. Walleye have been documented preying upon juvenile Colorado pikeminnow within the study area of this project (Francis and Ryden 2015, Francis 2019) and are likely the cause of decreased juvenile Colorado pikeminnow abundance in the Green River (Bestgen et al. 2018). In 2014, nonnative removal effort was reallocated to the lower reach of the Colorado River to address the expanding walleye population. While recruitment of Colorado pikeminnow has occurred since the establishment of the walleye population in the lower reach, the extent of impacts on adult fish from competition with walleye are unknown. Projects targeting problematic nonnative species within and adjacent to the Colorado pikeminnow habitat will continue to be necessary to prevent establishment of new populations of problematic nonnative species and to minimize the impacts of currently established species.

Razorback Suckers

The population estimates for razorback sucker indicate an increasing number of these fish are being captured in the Colorado River during sampling for Colorado pikeminnow. The most recent estimate (2015) for the entire study area show a significant increase in the number of razorback sucker when compared to all other years except 2014. Years 2013 and 2014 are significantly high than 2008 only. Most reach specific estimates have over-lapping CIs, but an increasing trend is evident in both the upper and lower reach. The CVs associated with the combined reach estimates for each year in the most recent study period were less 15%, indicating an acceptable level of precision. Razorback sucker survival estimates were not significantly different across years, but survival did increase with razorback sucker total length. In the most recent Green River study, razorback sucker survival was not found to be influence by total length (Zelasko et al. 2018). In 2013, sampling for this project resulted in the capture of 41 untagged, suspected wild-produced razorback suckers less than 250 mm TL. Only one of those 41 fish has been recaptured and it was identified as a razorback/flannelmouth hybrid. While suspected wild-produced razorback suckers have been captured during this project, the vast majority and possibly all of the razorback suckers in these estimates are likely the result of stocking hatchery produced razorback sucker. While the increasing abundance of razorback suckers is not the result of wild recruitment, the estimates do indicate that stocking of razorback suckers is continuing to result in an increase in their abundance river-wide.

SUMMARY AND CONCLUSIONS

- The Colorado River population of Colorado pikeminnow displayed a significant positive trend in annual abundance estimates for fish $\geq$ 450 mm TL from 1992 through 2005, but then significantly declined in abundance. In 1992, the combined-reach point estimate was 440; in 2005, 889; in 2015, 428.
- The minimum AIC$_c$ model for the new 2004–2015 capture history matrix differed from that of the minimum AIC$_c$ model for the 1991–2005 matrix. The earlier model included a reach effect on survival and fish total length as a quadratic model, but no time effect. The recent model included a reach effect on survival but no fish total length or time effect. Initial capture probabilities were reach- and time-specific for both primary and secondary occasions, but unlike the earlier model, were not length specific.
- Capture probability in the upper reach was significantly higher earlier in the study (1991–2000) than in more recent years (2003–2015).
- Annual survival rate was significantly higher in the upper reach than in the lower reach. In the upper reach, estimates of annual survival for each multi-year sampling period were similar, ranging from 85.9% to 89.0%. In the lower reach, there appeared to be a downward trend in survival rate estimates from 81.5% (1991–1994) to 76.1% (2013–2015).
- During the 25-year study period, the population remained self-sustaining. This was evidenced by: annual abundance estimates of sub-adults (400–449 mm TL) about to recruit that indicated recruitment roughly balanced estimated adult mortality in years for which data were available.

-- Results of efforts to link pulses of Colorado pikeminnow estimated as age-5 (mean length approximately 376 mm) to individual year-classes suggested that catch rates of YOY may not be reliable predictors of later recruitment levels in the Colorado River. Environmental factors that influence survival of juvenile age-classes may be as important in determining later recruitment as factors that influence levels of larval production and survival of early life stages.

-- To date, the Colorado River population of Colorado pikeminnow has remained self-sustaining, the only such population to do so besides the Green River population. As such, it is an important element of species recovery efforts. The primary impediment to long-term increases in abundance appears to be a low frequency of strong and moderately-strong recruitment years. Environmental factors that influence recruitment strength are poorly understood for the Colorado population.

RECOMMENDATIONS

1) We recommend that mark-recapture studies be continued in the upper Colorado River as the primary means of assessing trends of the Colorado pikeminnow population.
2) We recommend that the current regimen of sampling in three consecutive years followed by two years of no sampling be continued.
3) Investigate the possibility of utilizing portable PIT tag antennae in future estimates to increase precision.
4) We recommend initiating a study that develops a more reliable means of determining the year of origin of individuals 325–450 mm TL. Understanding environmental factors responsible for variation in recruitment strength begins with the ability to link recruit-sized fish to a particular year-class so that year-to-year abundance and survival of a given cohort can be tracked through time. Increasing the frequency of years with strong recruitment is the key to recovering this population.

5) Beginning in 2010, large numbers of walleye have been encountered in the lower reach during this project. Nonnative removal effort has been dedicated to removing walleye from the lower reach since 2013. Walleye have been documented preying upon Colorado pikeminnow and we recommend continuing walleye removal in the lower Colorado along with researching additional methods to increase the efficacy of walleye removal efforts in the lower Colorado River.

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Table 1. Number of captures of Colorado pikeminnow $\geq$ 250 mm TL captured in each sampling pass by year in the Colorado River study area, Colorado and Utah, 1991–2015. Totals include recaptures of fish caught in previous passes of the same year (parentheses). Captures are partitioned by upper and lower reach (see text) because abundance estimates were reach-specific.

Year	Lower Reach Sampling Passes					Upper Reach Sampling Passes				
	1	2	3	4	5	1	2	3	4	5
1991	37	---	---	---	---	23	17 (4)	25 (2)	---	---
1992	18	15 (1)	---	---	---	21	24 (2)	23 (2)	---	---
1993	51	41 (4)	---	---	---	31	31 (6)	33 (11)	---	---
1994	47	22 (3)	---	---	---	28	37 (3)	38 (6)	---	---
1998	31	56 (6)	---	---	---	47	73 (8)	55 (16)	---	---
1999	38	24 (2)	---	---	---	52	65 (8)	54 (18)	---	---
2000	31	19 (1)	---	---	---	51	52 (8)	28 (6)	---	---
2003	11	16 (0)	44 (0)	40 (2)	---	11	15 (0)	16 (2)	11 (1)	---
2004	28	36 (1)	27 (0)	---	---	19	16 (2)	48 (8)	---	---
2005	26	50 (3)	46 (7)	36 (6)	34 (5)	22	30 (4)	26 (4)	46 (5)	38 (9)
2008	13	29 (0)	35 (3)	23 (7)	---	17	15 (0)	17 (1)	20 (2)	16 (2)
2009	11	35 (0)	28 (3)	21 (4)	---	10	13 (0)	32 (0)	15 (2)	23 (9)
2010	19	14 (1)	35 (5)	37 (6)	---	14	19 (1)	15 (1)	22 (3)	17 (2)
2013	17	31 (0)	25 (4)	---	---	15	10 (1)	12 (1)	14 (5)	---
2014	45	60 (4)	16 (4)	35 (6)	---	13	18 (0)	16 (4)	21 (7)	15 (3)
2015	34	45 (0)	45(5)	30 (7)	---	10	15 (2)	16 (0)	15 (4)	13 (2)

Table 2. Estimates for the von Bertalanffy growth curve for Colorado pikeminnow in the Colorado River study area, 2004–2015. *K* is the von Bertalanffy growth coefficient; L_∞ is the asymptotic length.

Parameter	Estimate	Standard error	95% CI (lower)	95% CI (upper)
K	0.079	0.00493	0.0694	0.0887
L_∞	830.4	13.9157	803.0	857.8

Table 3. Model selection results of the robust design multi-state model for Colorado pikeminnow in the upper Colorado River (2004–2015). Abbreviations include: Survival (*S*), transition or movement rates between reaches (ψ), probability of capture (*p*), and fish total length (TL).

Model	AIC_c	ΔAIC_c	AIC_c Weights	No. Parameters	Deviance
{S(reach) ψ(reach*TL) p(reach*year*pass) DM}	8361.1532	0	0.44319	77	8199.63
{S(reach) ψ(reach*TL^2) p(reach*year*pass) DM}	8362.0683	0.9151	0.28047	79	8196.14
{S(reach+TL) ψ (reach*TL) p(reach*year*pass) DM}	8363.2588	2.1056	0.15466	78	8199.54
{S(reach) ψ(reach*TL) p(reach*year*pass+reach*TL) DM}	8363.7524	2.5992	0.12083	79	8197.83
{S(reach) ψ(reach) p(reach*year*pass) DM}	8375.7351	14.5819	0.0003	75	8218.61
{S(reach) ψ(reach) p(reach*year*pass+TL) DM}	8376.227	15.0738	0.00024	76	8216.90
{S(reach+TL) ψ (reach) p(reach*year*pass) DM}	8377.7918	16.6386	0.00011	76	8218.47
{S(reach) ψ(reach) p(reach*year*pass+reach*TL) DM}	8378.4205	17.2673	0.00008	77	8216.90
{S(reach*TL) ψ (reach) p(reach*year*pass) DM}	8379.283	18.1298	0.00005	77	8217.76
{S(reach+TL^2) psi(reach) p(reach*year*pass) DM}	8379.8027	18.6495	0.00004	77	8218.28
{S(reach) ψ(reach) p(reach*year*pass+reach*TL^2) DM}	8380.6961	19.5429	0.00003	79	8214.77
{S(reach*TL^2) ψ (reach) p(reach*year*pass) DM}	8383.1679	22.0147	0.00001	79	8217.24
{S(reach) ψ(reach*year) p(reach*year*pass) DM}	8384.7037	23.5505	0	87	8201.06
{S(reach) ψ(reach) p(reach*year+reach*pass) DM}	8389.008	27.8548	0	28	8332.02
{S(reach) ψ(reach) p(reach*year+pass) DM}	8400.6736	39.5204	0	24	8351.95
{S(reach) ψ(reach) p(reach*year)}	8424.4805	63.3273	0	20	8383.97
{S(reach) ψ(reach) p(reach*year) DM}	8424.4805	63.3273	0	20	8383.97
{S(reach+year) ψ(reach) p(reach*year) DM}	8432.5128	71.3596	0	26	8379.66
{S(reach*year) ψ(reach) p(reach*year) DM}	8438.8198	77.6666	0	32	8373.53

Table 4. Model selection results of the robust design multi-state model (for the top 10 models only) for Colorado pikeminnow in the upper Colorado River (1991-2005). Survival (S), reach (reach), transition or movement rates between reaches (ψ), probability of capture (p), and fish total length (length). Other covariates considered in these models include primary and secondary occasion time effects, river flow (CFS), water temperature, and number of boat days as a measure of effort to predict capture probability. Parameters modeled with length^2 include both a linear and quadratic term for length. All recapture probabilities (c) were assumed equal to initial capture probabilities (p). The third and fourth ranked models denoted 'ADDED' are post hoc models that were developed in response to the transition analysis in Osmundson and White 2009.

Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ Weights	No. Parameters	Deviance
{S(reach+length^2) ψ(reach*t+reach*length) p(reach*primary*t+length^2)=c DM}	8306.75	0.00	0.36	83	8133.12
{S(reach+length^2) ψ(reach*t+reach*length) p(reach*primary*t+length)=c DM}	8306.88	0.13	0.33	82	8135.43
{ADDED {S(reach+length^2) ψ(reach*t+reach*length^2 + quad spline) p(reach*primary*t+length^2)=c DM}	8308.72	1.97	0.13	87	8126.33
{ADDED {S(reach+length^2) ψ(reach*t+reach*length linear spline) p(reach*primary*t+length^2)=c DM}	8308.86	2.10	0.12	85	8130.85
{S(reach+length^2) ψ(reach*t) p(reach*primary*t+length)=c DM}	8313.56	6.81	0.01	80	8146.48
{S(reach+length^2) ψ(reach*t) p(reach*primary*t+length^2)=c DM}	8313.61	6.85	0.01	81	8144.34
{S(reach+length^2) ψ(reach*t+reach*length^2) p(reach*primary*t+length)=c DM}	8313.80	7.05	0.01	84	8137.98
{S(reach+length^2) ψ(reach*t+length^2) p(reach*primary*t+length)=c DM}	8315.17	8.42	0.01	82	8143.73
{S(reach+length^2) ψ(reach*t) p(reach*primary*t)=c DM}	8315.20	8.45	0.00	79	8150.30
{S(reach+GE(length,500)) ψ(reach*t+length) p(reach*primary*t+length^2)=c DM}	8316.84	10.09	0.00	81	8147.58

Table 5. Annual (1991–2014) transition probabilities for Colorado pikeminnow 500 mm TL moving from one study reach to the other as estimated by the top ranked model in Table 3.

Start year	End Year	From lower to upper reach	From upper to lower reach	Net movement to upper reach
1991	1992	0.0000	0.0000	0.0000
1992	1993	0.2431	0.0000	0.2431
1993	1994	0.2320	0.0000	0.2320
1994	1995	0.1990[1]	0.0000[1]	0.1990[1]
1995	1996	0.1990[1]	0.0000[1]	0.1990[1]
1996	1997	0.1990[1]	0.0000[1]	0.1990[1]
1997	1998	0.1990[1]	0.0000[1]	0.1990[1]
1998	1999	0.0000	0.0000	0.0000
1999	2000	0.0461	0.1580	-0.1119
2000	2001	0.0000[2]	0.0900[2]	-0.0900[2]
2001	2002	0.0000[2]	0.0900[2]	-0.0900[2]
2002	2003	0.0000[2]	0.0900[2]	-0.0900[2]
2003	2004	0.0563	0.0000	0.0563
2004	2005	0.3046	0.0000	0.3046
2005	2006	0.0735[3]	0.0692	0. 0043
2006	2007	0.0735[3]	0.0692	0. 0043
2007	2008	0.0735[3]	0.0692	0. 0043
2008	2009	0.0735[3]	0.0692	0.0043
2009	2010	0.0735[3]	0.0692	0.0043
2010	2011	0.0735[3]	0.0692	0.0043
2011	2012	0.0735[3]	0.0692	0.0043
2012	2013	0.0735[3]	0.0692	0.0043
2013	2014	0.0735[3]	0.0692	0.0043
2014	2015	0.0735[3]	0.0692	0.0043

[1] Average per year calculated from single value for period 1994–1998; no capture data available for these individual un-sampled years; annual estimates for these years might be higher or lower than average value provided.

[2] Average per year calculated from single value for period 1998–2000 because of un-sampled years

[3] Values for the last two periods are identical because top model indicated no time effect.

Table 6. Qualitative estimates of Colorado pikeminnow year-class strength based on length-frequency histograms of samples collected from the Colorado River lower-reach study area, 1991–1994, 1998–2000, 2003–2005, 2008–2010, and 2013–2015. Strength of the age-5 cohort is based on its percentage of the total sample collected: Weak = 0-15%; Moderate-strength =16-50%; Strong = 51-100%.

Year of origin	Length frequency year	Length range of Age-5 (mm)	Number in age-5 group	Lower-reach Sample (n)	Age-5 as percent of total (%)	Mean Length age-5 (mm)	Year-class strength
1986	1991	325-401	28	37	76	363	Strong
1987	1992	320-380	6	32	19	365	Moderate
1988	1993	345-416	5	88	6	382	Weak
1989	1994	353-446	8	66	12	386	Weak
1990	1995						Weak[1]
1991	1996						Moderate[2]
1992	1997						Moderate[3]
1993	1998	334-389	15	86	17	365	Moderate
1994	1999	343-382	5	60	8	360	Weak
1995	2000	400-420	3	49	6	412	Weak
1996	2001						Weak[4]
1997	2002						Weak[5]
1998	2003	325-435	70	109	64	387	Strong
1999	2004	347-411	11	110	10	387	Weak
2000	2005	334-432	24	143	17	374	Moderate
2001	2006						Weak[6]
2002	2007						Weak[7]
2003	2008	397-442	6	89	7	416	Weak
2004	2009	374-448	4	81	5	409	Weak
2005	2010	327-409	25	92	27	367	Moderate
2006	2011						Weak[8]
2007	2012						Weak[9]
2008	2013	371-450	51	80	64	413	Strong
2009	2014	376-419	7	145	5	396	Weak
2010	2015	365-435	45	142	32	393	Moderate

[1] Year-class strength category estimate based on the relative rarity of age-4 fish in 1994.

[2] Year-class strength category estimate based on relative abundance of age-7 fish in 1998.

[3] Year-class strength category estimate based on relative abundance of age-6 fish in 1998 and age-7 fish in 1999

[4] Year-class strength category estimate based on relative rarity of age-7 fish in 2003.

[5] Year-class strength category estimate based on relative rarity of age-6 fish in 2003.

[6] Year-class strength category estimate based on relative rarity of age-4 fish in 2005 and age-7 fish in 2008.

[7] Year-class strength category estimate based on relative rarity of age-6 fish in 2008.

[8] Year-class strength category estimate based on relative rarity of age-4 fish in 2010.

[9] Year-class strength category estimate based on relative rarity of age-6 fish in 2013.

Table 7. Total number of Colorado pikeminnow encounters in upper basin rivers since use of PIT tags began in 1990. Values do not represent number of different fish captured, rather the number of encounters. Fish captured more than once on the same day are counted as only one capture. PIT tags were used in 1990 in the Colorado River but not in other rivers. Captures in other rivers in 1990, without use of PIT tags, are not shown. Captures recorded for the Gunnison River include fish above and below the Redlands Diversion Dam (RM 3.0). Capture records for 2004 and 2005 in the Colorado River do not include the capture of recently stocked fish. Note: Sampling locations and intensity vary by river and year. For example: the 0 captures for the White River in 2004 and 2005 are the result of no sampling occurring in the White River during those years.

Year	CO[1]	GU[2]	DO[3]	GR[4]	WH[5]	YA[6]	DU[7]	PR[8]	SR[9]	LS[10]	TOTAL
1990	23	0	0	0	0	0	0	0	0	0	**23**
1991	118	3	3	82	22	72	0	0	0	0	**300**
1992	133	4	0	142	19	53	0	0	0	0	**351**
1993	209	10	0	114	72	42	7	0	0	0	**454**
1994	209	42	0	208	34	19	0	0	0	0	**512**
1995	117	20	0	442	38	21	0	1	0	3	**642**
1996	124	16	0	299	42	42	2	6	0	0	**531**
1997	133	22	0	327	60	23	9	11	0	0	**585**
1998	358	37	0	493	43	57	3	1	6	0	**998**
1999	266	15	0	356	72	63	25	2	0	0	**799**
2000	254	11	0	867	326	141	23	0	0	0	**1,622**
2001	39	3	0	952	239	235	0	0	0	0	**1,468**
2002	0	7	0	504	184	50	0	0	0	0	**745**
2003	187	7	0	388	121	67	0	0	0	0	**770**
2004	199	23	0	144	0	75	0	0	0	0	**441**
2005	363	8	0	157	0	56	0	0	0	0	**584**
2006	0	10	0	799	106	62	7	0	0	0	**984**
2007	3	23	0	720	136	52	0	0	1	0	**935**
2008	179	10	0	507	67	33	0	0	0	0	**796**
2009	186	13	0	229	11	119	0	0	0	0	**558**
2010	184	14	0	245	3	118	0	0	0	0	**564**
2011	13	2	0	789	95	83	0	0	0	0	**982**
2012	6	13	0	445	124	37	0	0	0	0	**625**
2013	284	6	0	338	74	44	0	0	0	0	**746**
2014	305	22	0	132	18	32	0	0	0	0	**509**
2015	250	9	0	128	15	47	0	0	0	0	**449**
Total	**4,142**	**350**	**3**	**9,807**	**1,921**	**1,643**	**76**	**21**	**7**	**3**	

[1] Colorado River

[2] Gunnison River

[3] Dolores River

[4] Green River

[5] White River

[6] Yampa River

[7] Duchesne River

[8] Price River

[9] San Rafael River

[10] Little Snake River

Table 8. Model selection results of the robust design multi-state model for Razorback sucker in the upper Colorado River (2008–2015). Abbreviations include: Survival (*S*), transition or movement rates between reaches (ψ), probability of capture (*p*), and fish total length (TL). Also considered as covariates in these models were primary and secondary occasion time effects.

Model	AICc	ΔAIC_c	AIC_c Weights	No. Parameters	Deviance
{S(reach+TL) ψ(reach) p(reach*pass*year)=c DM}	15983.2521	0	0.50282	56	15869.71
{S(reach+TL^2) ψ(reach) p(reach*pass*year)=c DM}	15983.2747	0.0226	0.49718	57	15867.67
{S(reach) ψ(reach) p(reach*pass*year)=c DM}	16037.1825	53.9304	0	55	15925.69
{S(reach) ψ(reach+TL) p(reach*pass*year)=c DM}	16039.8407	56.5886	0	57	15924.24
{S(reach*pass) ψ(reach) p(reach*pass*year)=c}	16049.1736	65.9215	0	70	15906.76
{S(reach*pass) ψ(reach*pass) p(reach*pass*year)=c}	16054.2457	70.9936	0	78	15895.25
{S(.) ψ(reach) p(reach*pass*year)=c}	16063.5479	80.2958	0	59	15943.83
{S(pass) ψ(reach) p(reach*pass*year)=c}	16069.6413	86.3892	0	63	15941.69
{S(reach) ψ(reach) p(reach*pass)=c(reach*pass)}	16989.1575	1005.9054	0	16	16957.03

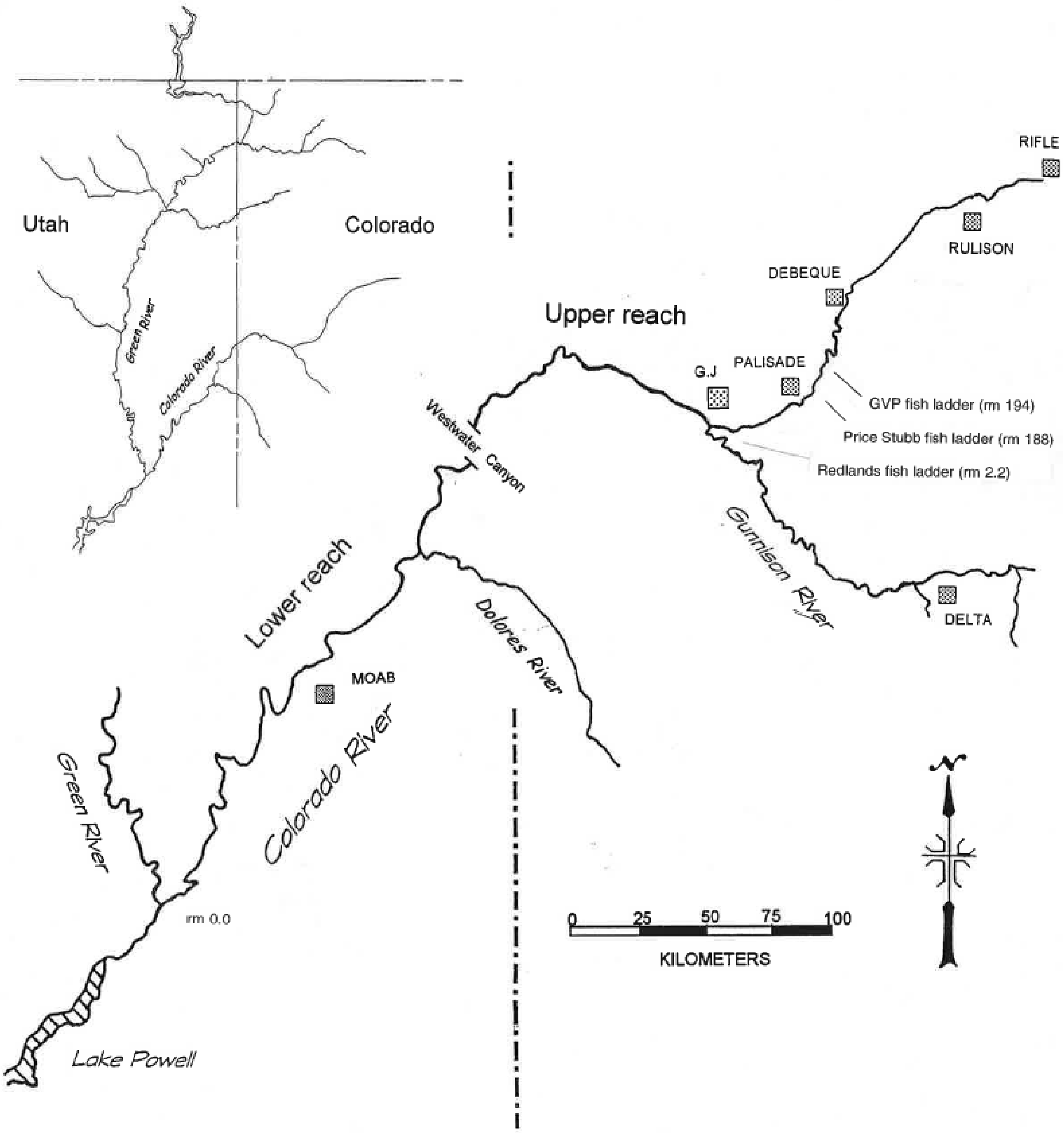


Figure 1. Map of the upper and lower reaches of the Colorado River study area. The downstream boundary of the lower reach was the confluence with the Green River (RM 0.0) and the upstream boundary was the lower end of Westwater Canyon (RM 112). The downstream boundary of the upper reach was the upper end of Westwater Canyon (RM 124) and the upstream boundaries were the fish ladders (Price Stubb and GVPDD) at RM 188 (1991–2005) and RM 193.7 (2008–2010 and 2013–2015; see text) on the Colorado River and the Redlands fish ladder at RM 2.2 on the Gunnison River (all years). Grand Junction is abbreviated G.J.; Grand Valley Project (diversion dam) is GVPDD.

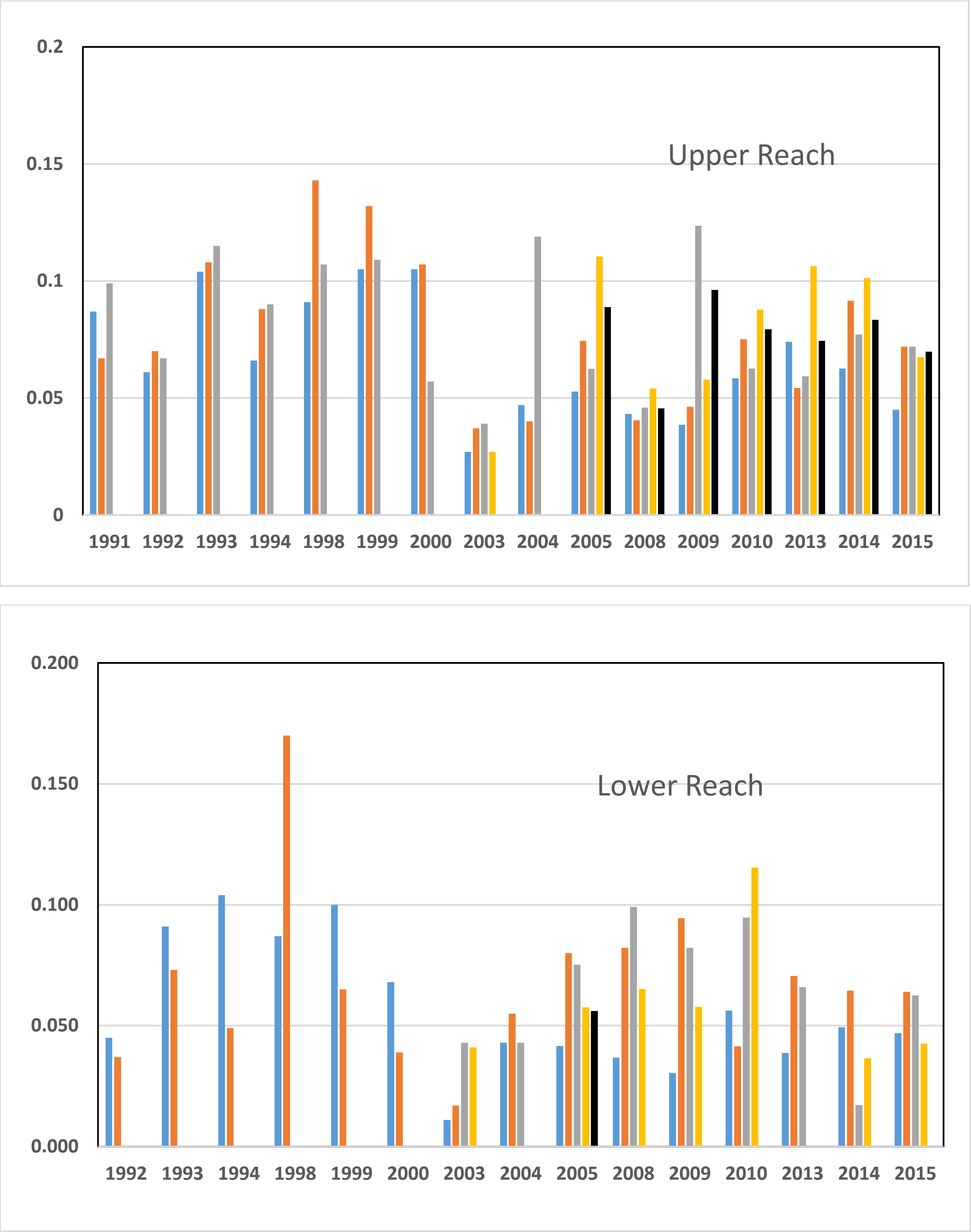


Figure 2. Capture probability by pass in the upper (top panel) and lower (bottom panel) reaches for a Colorado pikeminnow with a length standardized at 500 mm TL. Each bar represents a separate sampling pass. Passes are grouped by year: pass 1: blue; pass 2: orange; pass3: gray; pass 4: yellow; pass 5: black.

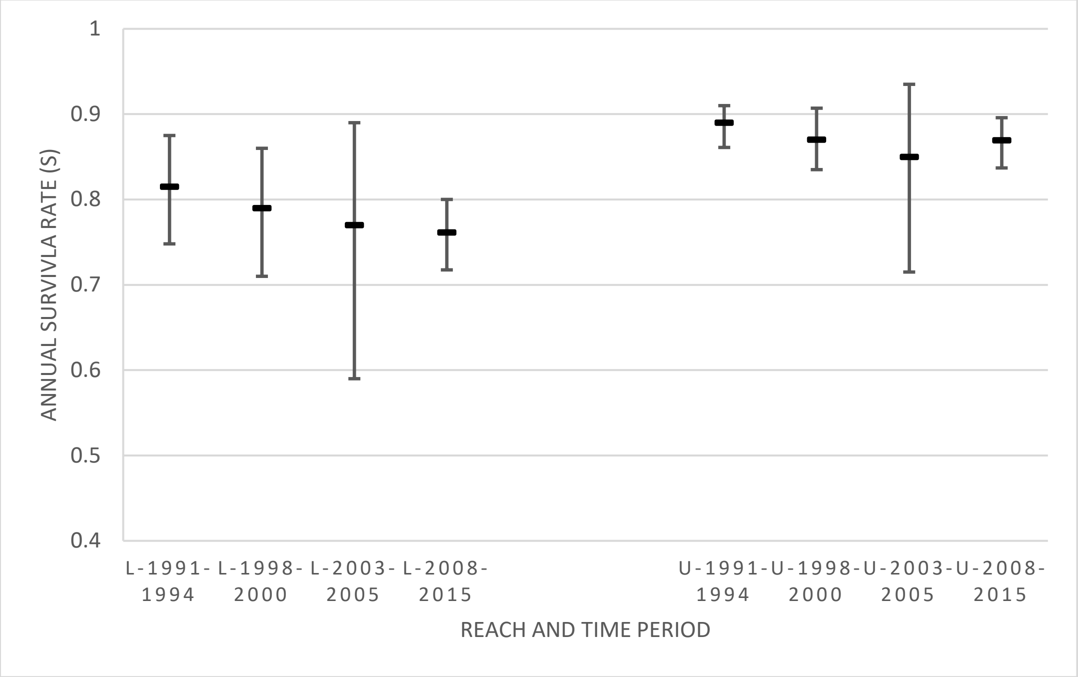


Figure 3. Annual survival rate (*S*) estimates of Colorado pikeminnow ≥ 500 mm TL by reach (upper: U; lower: L) for the three earlier multi-year periods, and for Colorado pikeminnow > 250 mm TL for 2008–2015. Error bars represent the 95% confidence intervals.

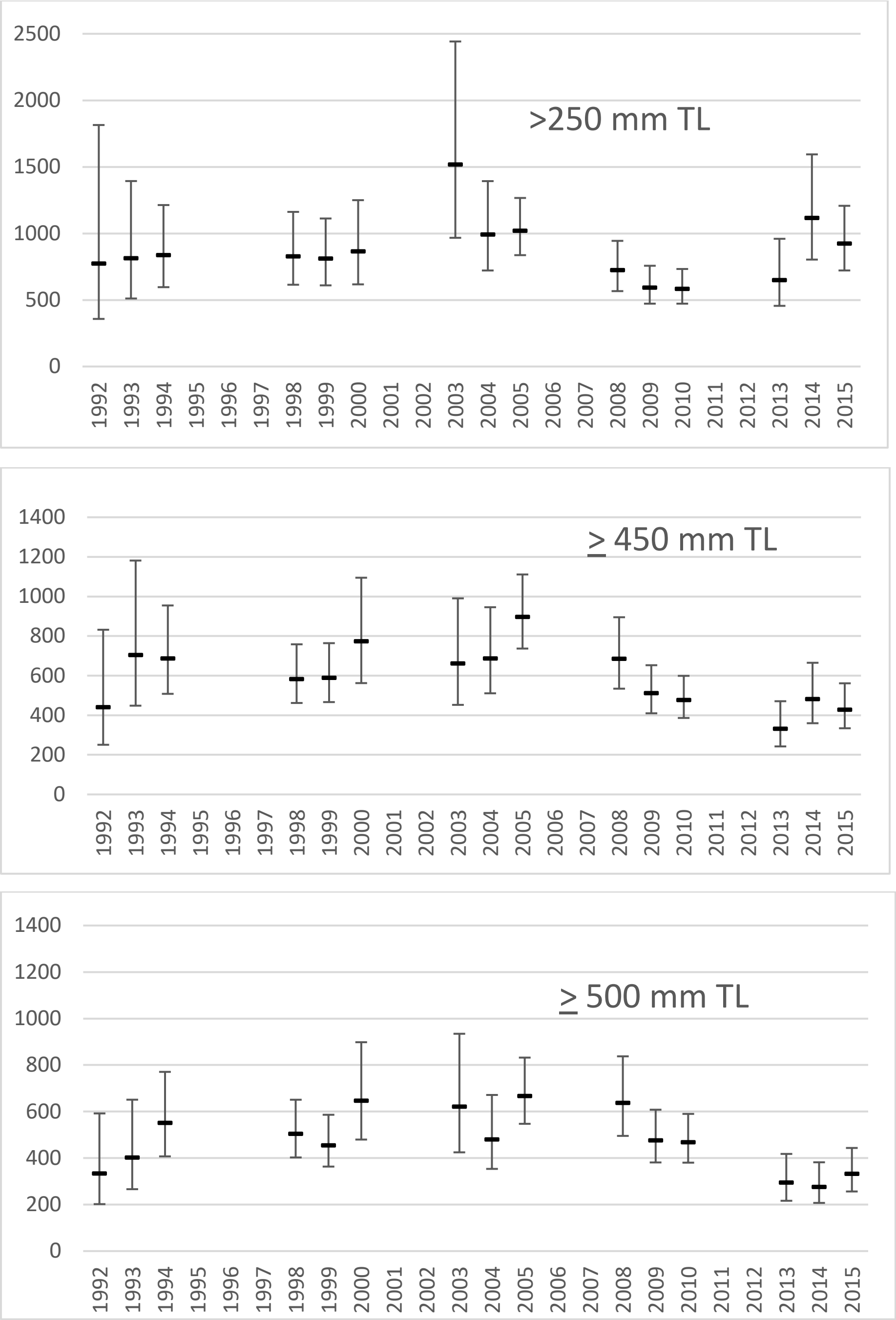


Figure 4. Abundance estimates of Colorado pikeminnow of three length classes: ≥ 250 mm TL; ≥ 450 mm TL; ≥ 500 mm TL in the upper Colorado River study area (reaches combined), 1992–2015. Annual population abundance estimates shown were derived by summing separate estimates for the lower and upper reaches (see Appendix Tables III, IV and V for numbers). Error bars represent the 95% confidence intervals.

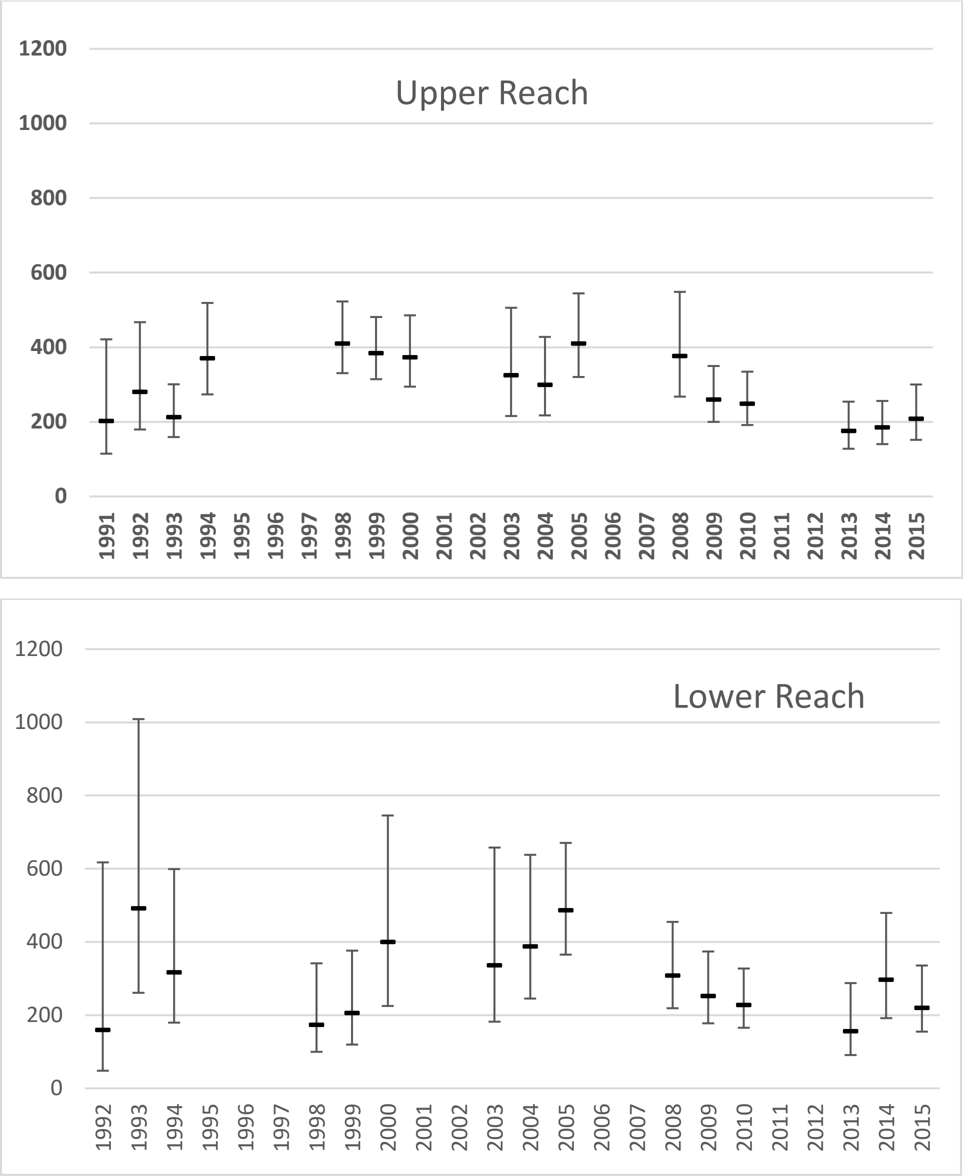


Figure 5. Abundance estimates of Colorado pikeminnow ≥ 450 mm TL in the upper (top panel) and lower (bottom panel) Colorado River study reaches, 1991–2015 (see Appendix Tables IV for numbers). Error bars represent the 95% confidence intervals.

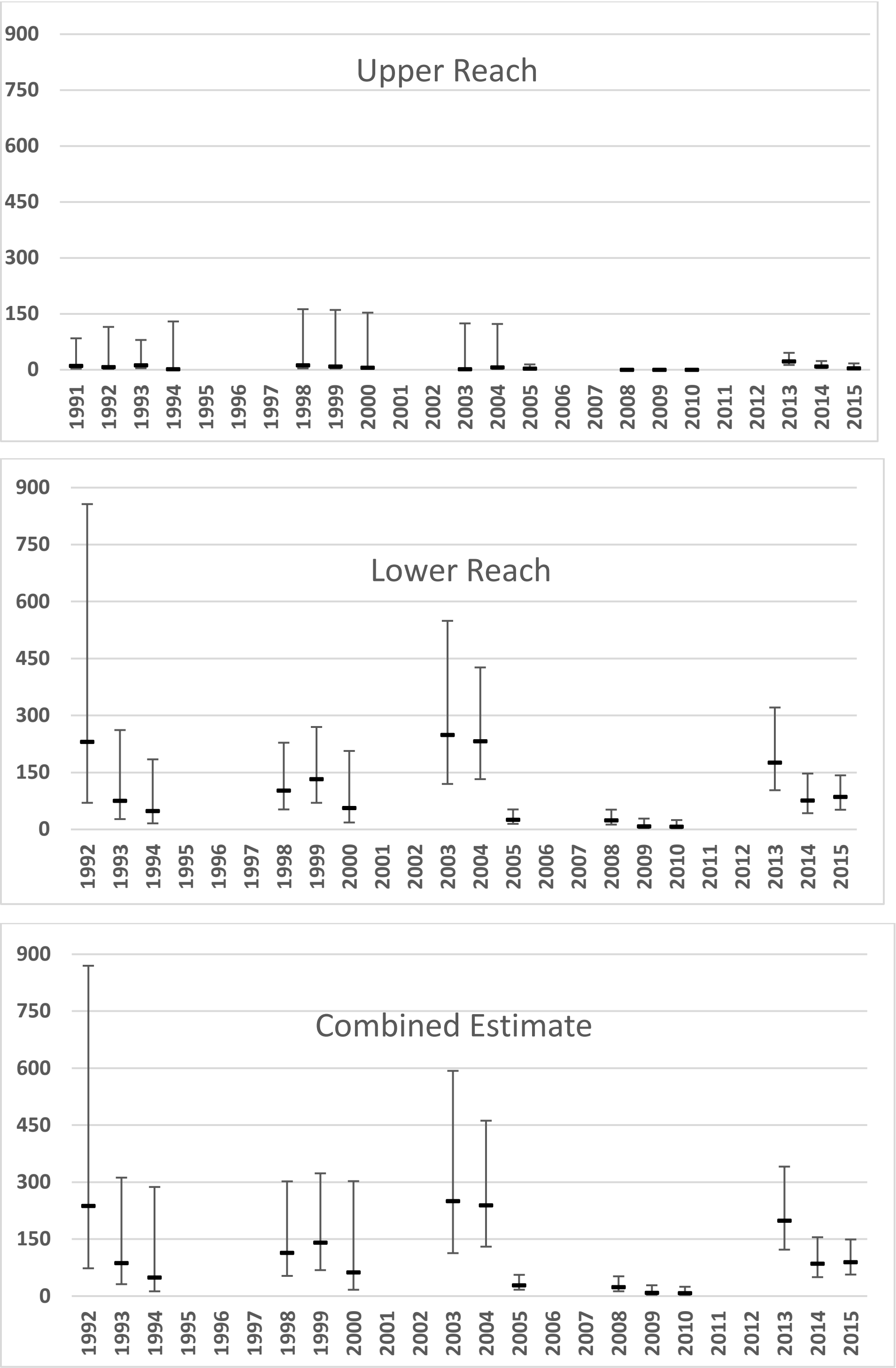


Figure 6. Annual abundance estimates of Colorado pikeminnow 400–449 mm TL in the upper, lower, and combined reaches, 1991–2015 (see Appendix Tables VI for numbers). Error bars represent the 95% confidence intervals.

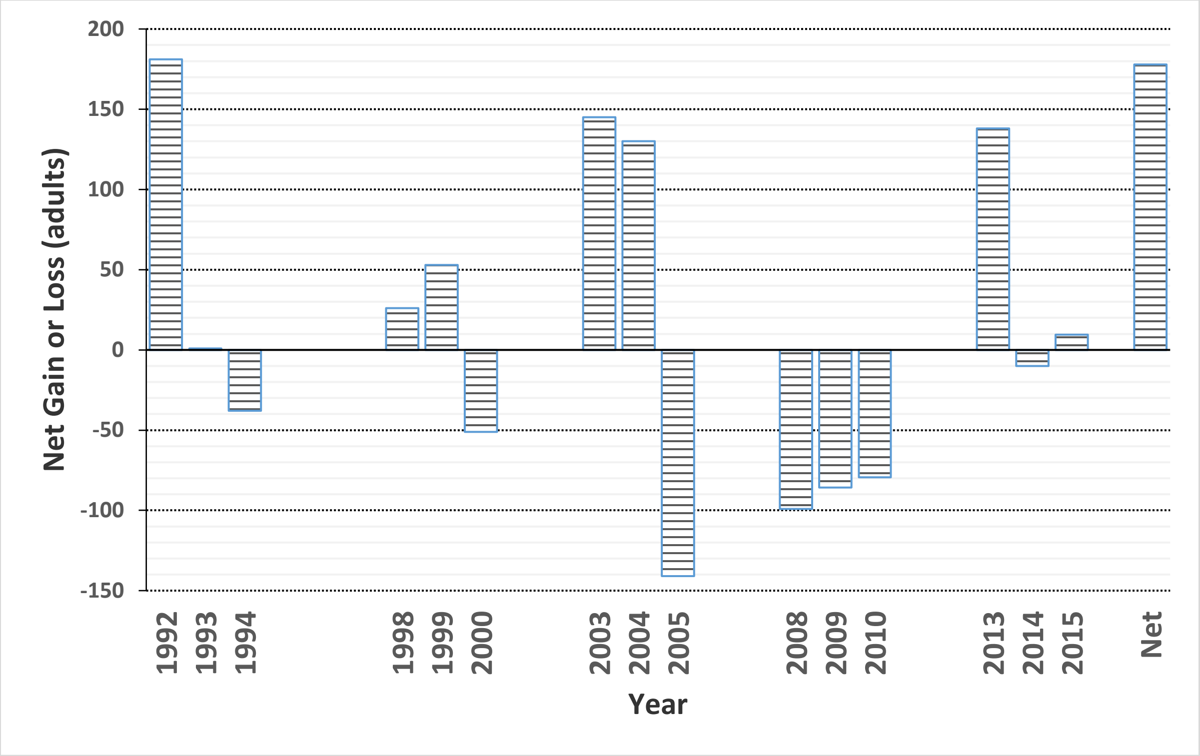
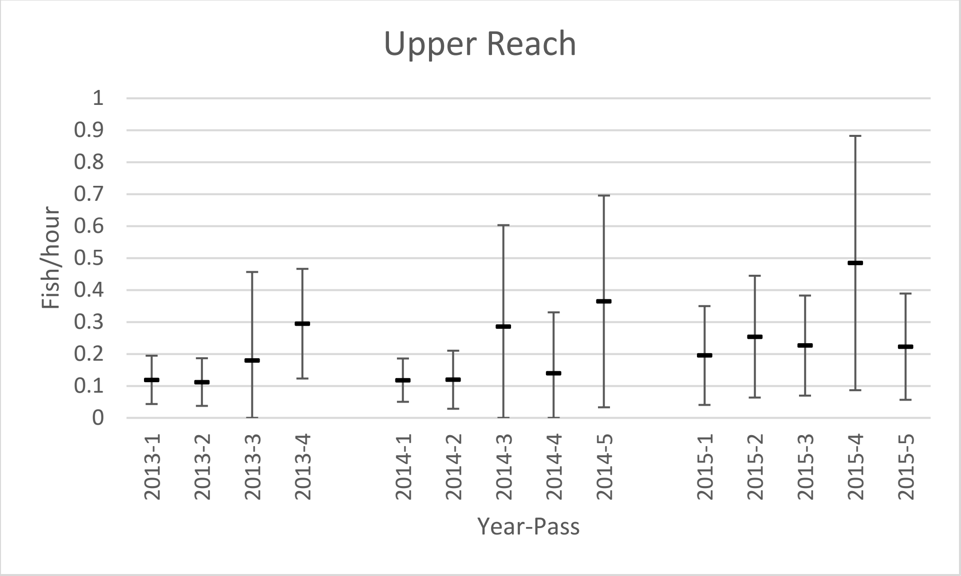


Figure 7. Estimated annual net gain or loss of Colorado pikeminnow ≥ 450 mm TL in the Colorado River population (upper and lower reaches combined). Values are based on the estimated number of fish 400–449 mm TL present each year minus the estimated number of deaths of fish ≥ 450 mm TL.



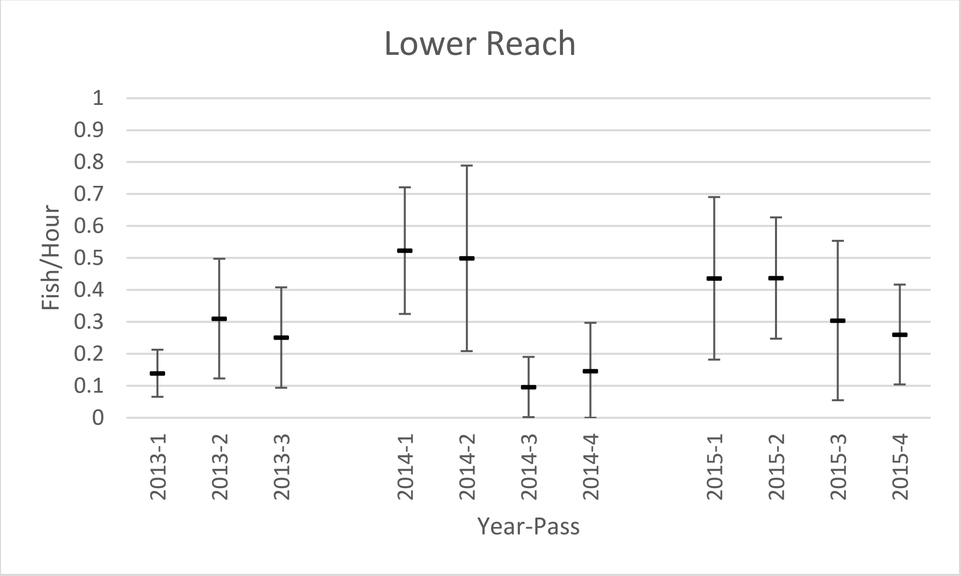


Figure 8. Mean electrofishing catch rates (fish/hr) of Colorado pikeminnow ($\geq$ 250 mm TL) by sampling pass in the upper (top) and lower (bottom) reaches of the Colorado River study area, 2013–2015. Error bars represent the 95% confidence intervals.

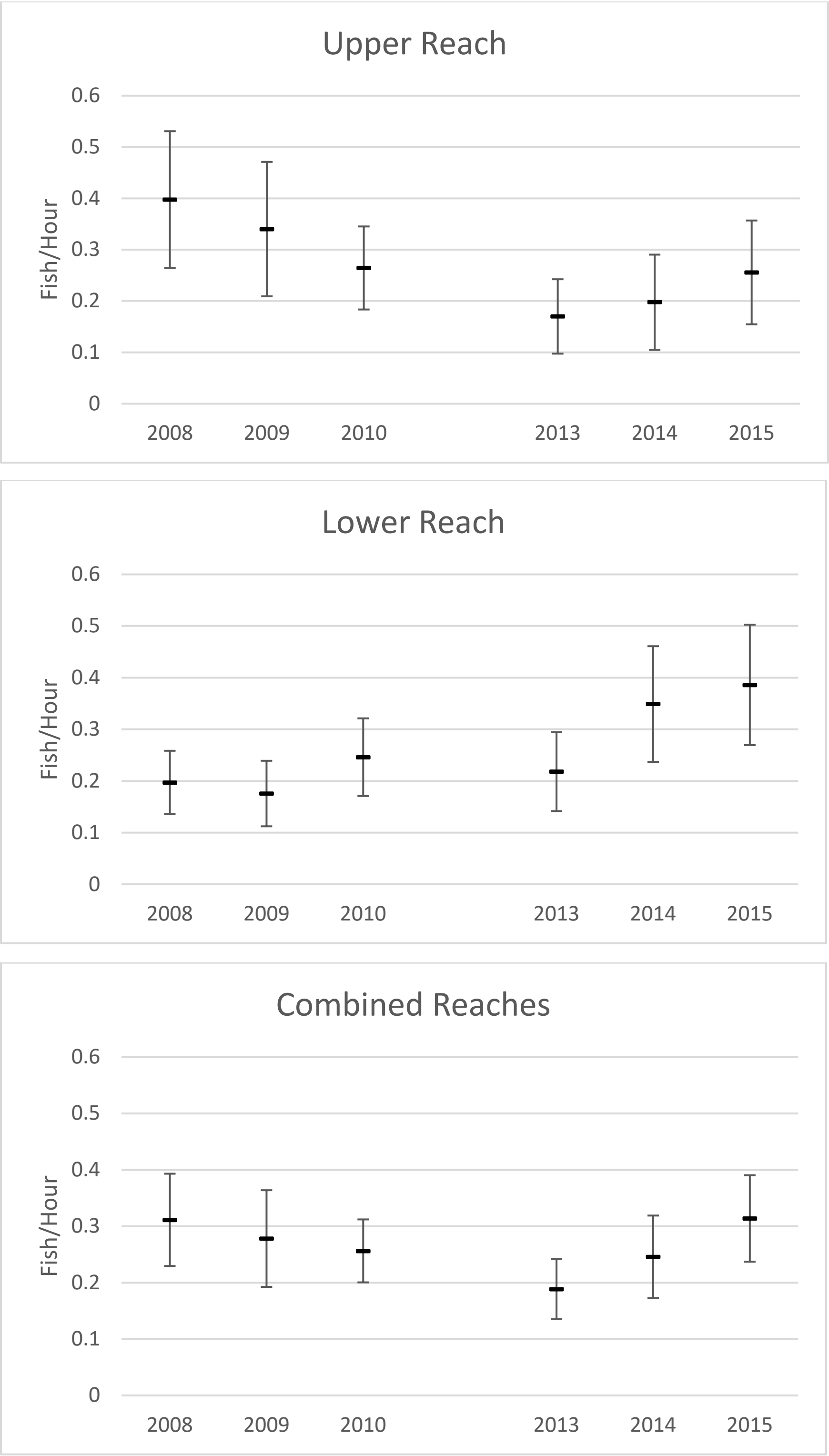


Figure 9. Mean electrofishing catch rates (fish/hr) of Colorado pikeminnow (≥ 250 mm TL) in the upper (top), lower (middle), and combined (bottom) reaches of the Colorado River study area, 2008–2010, and 2013–2015. Error bars represent the 95% confidence intervals.

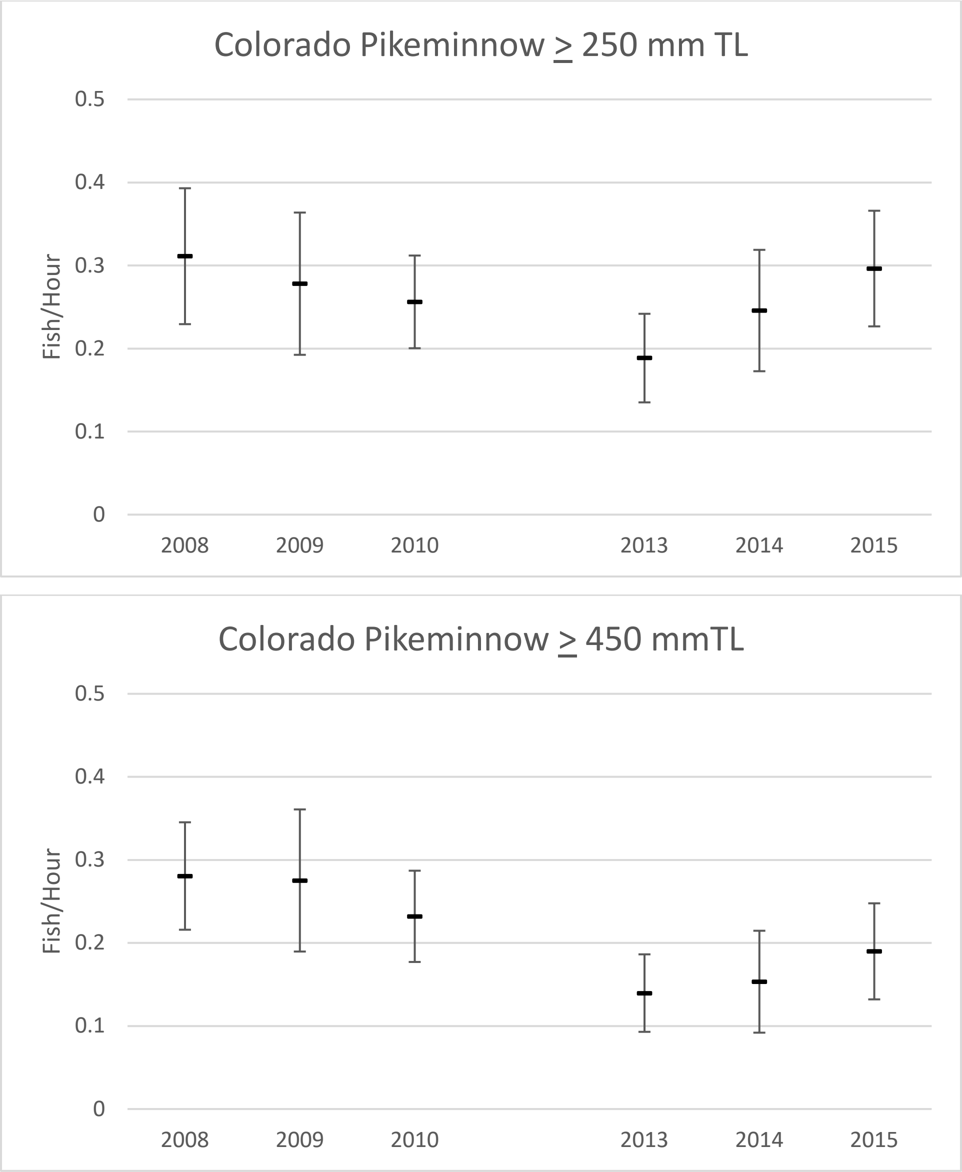


Figure 10. Mean electrofishing catch rates (fish/hr) of Colorado pikeminnow ≥ 250 mm TL and ≥ 450 mm TL. Data from the upper and lower reaches were combined to come up with mean annual rates for the entire Colorado River study area, 2008–2010, and 2013–2015. Error bars represent the 95% confidence intervals.

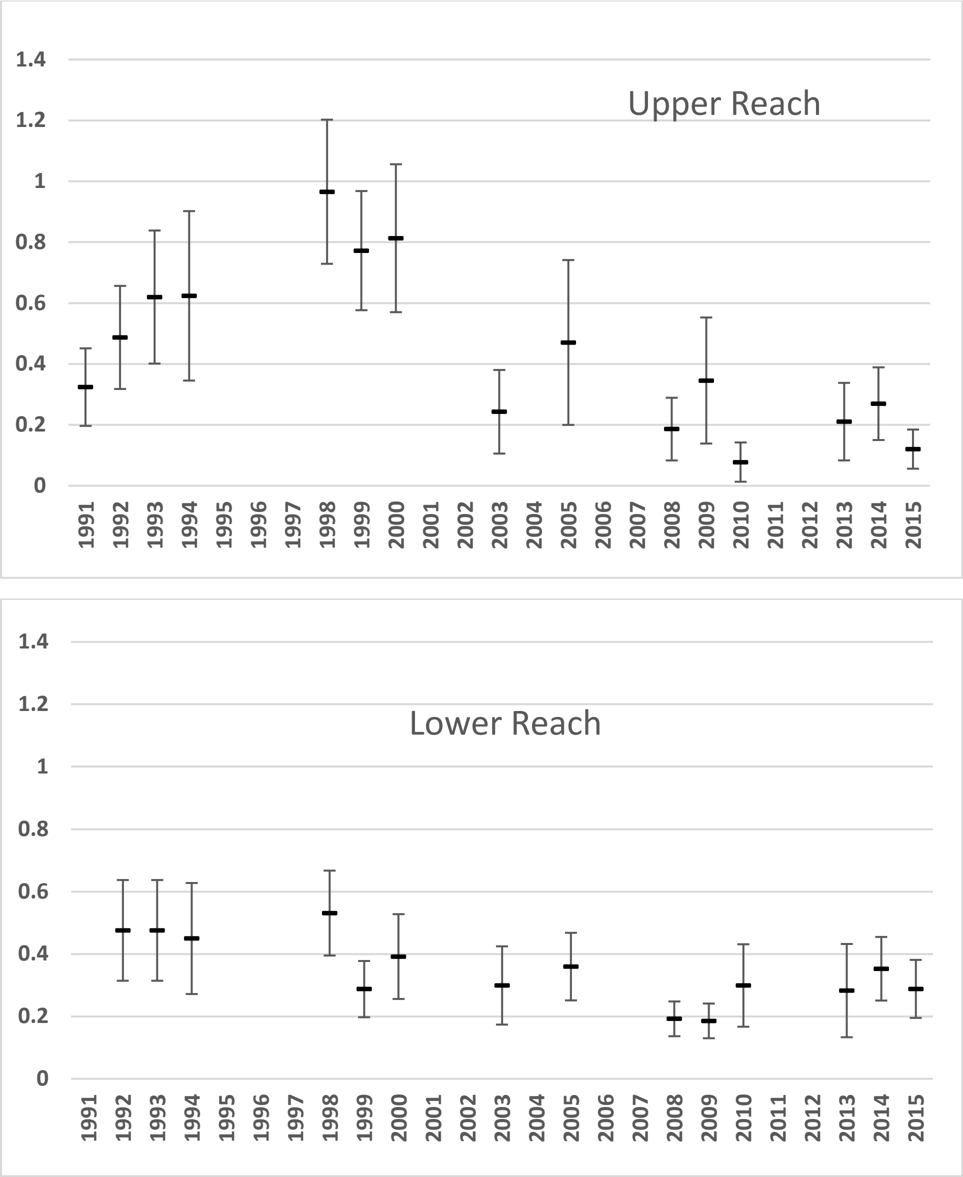


Figure 11. Trammel net catch rates (mean number of fish per net set) of Colorado pikeminnow in the lower and upper reach Colorado River study areas, 1991–2015. Error bars represent the 95% confidence intervals.

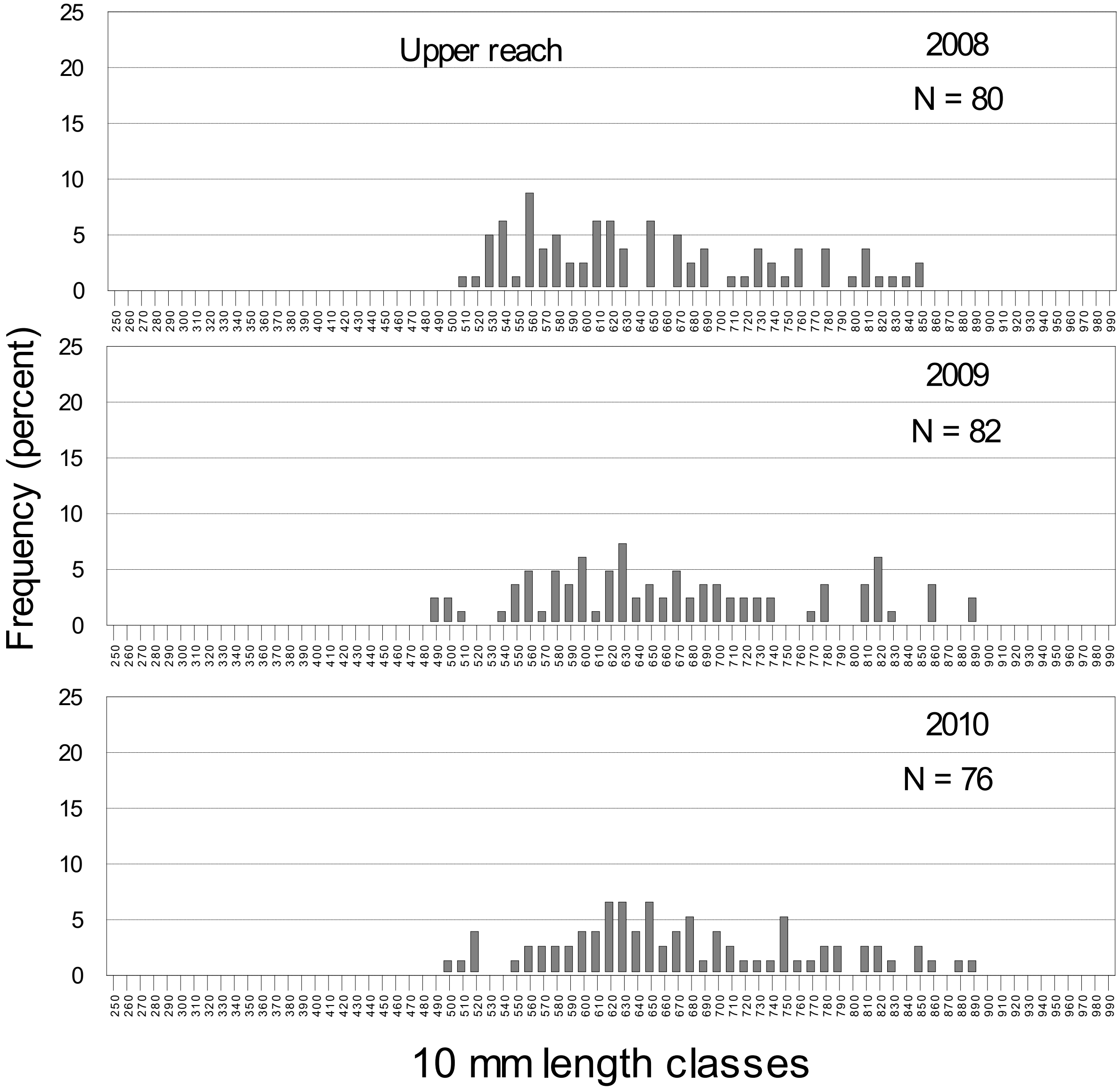


Figure 12. Length frequencies of Colorado pikeminnow captured in the upper Colorado River study reach, 2008–2010.

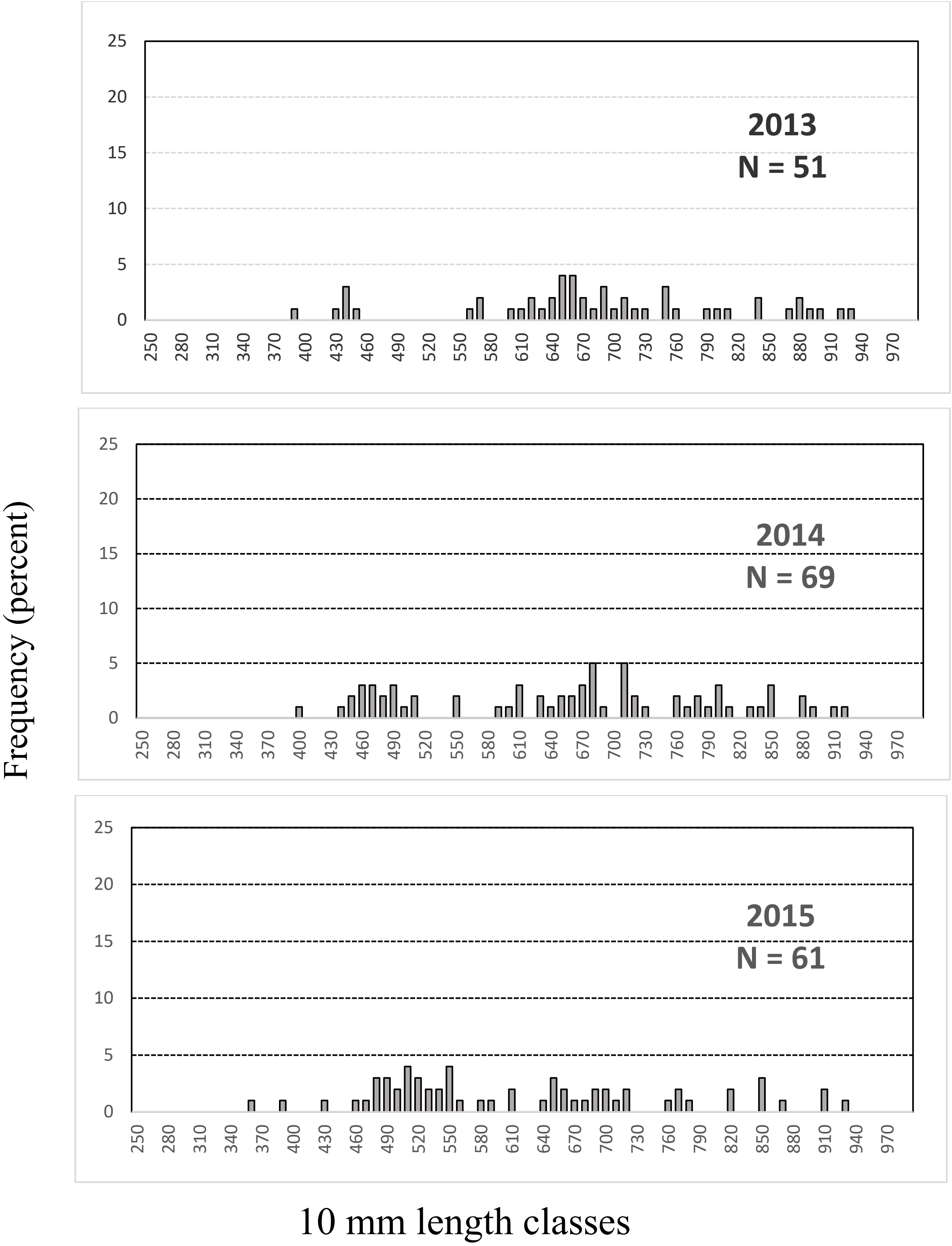


Figure 13. Length frequencies of Colorado pikeminnow captured in the upper Colorado River study reach, 2013–2015.

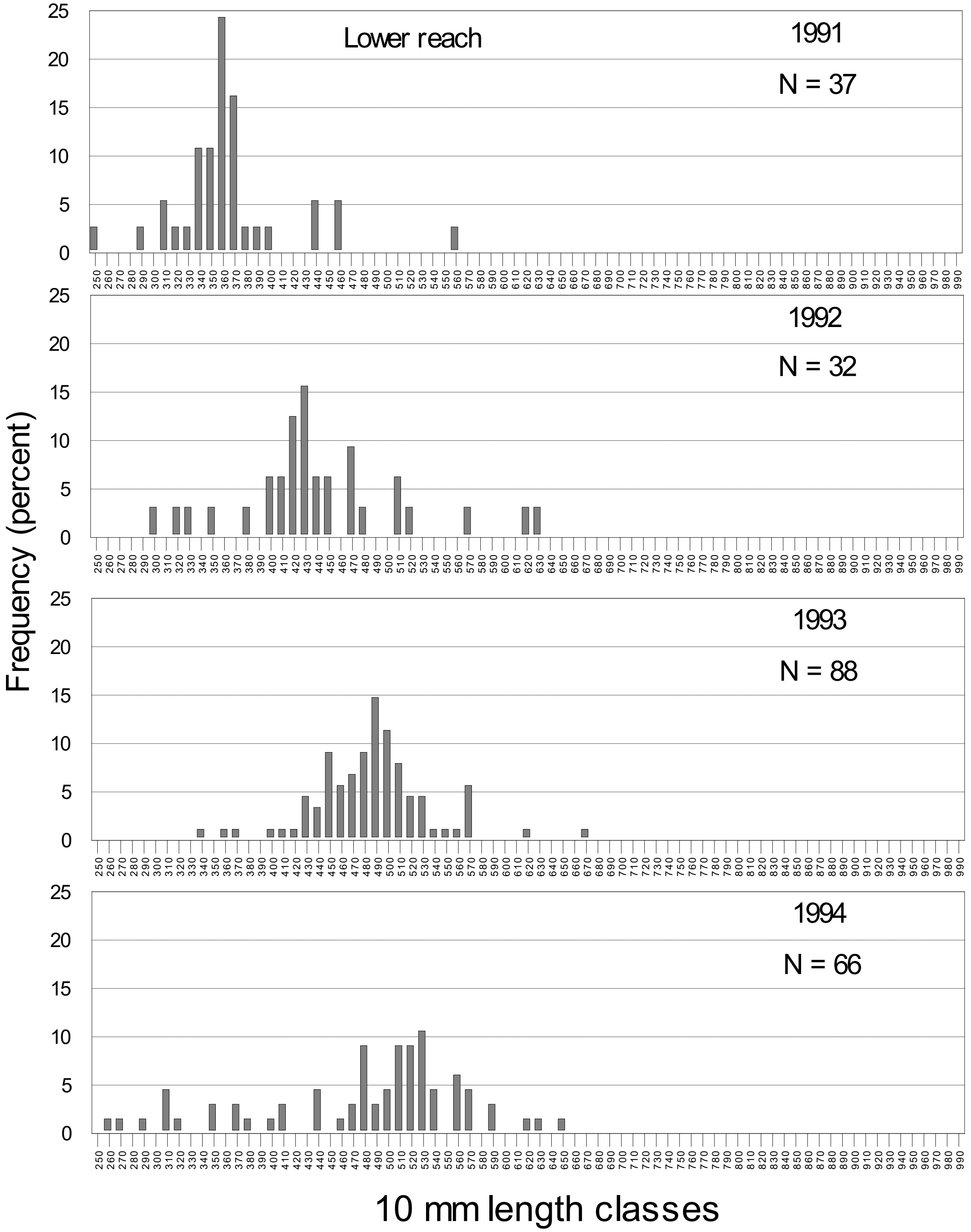


Figure 14. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 1991–1994.

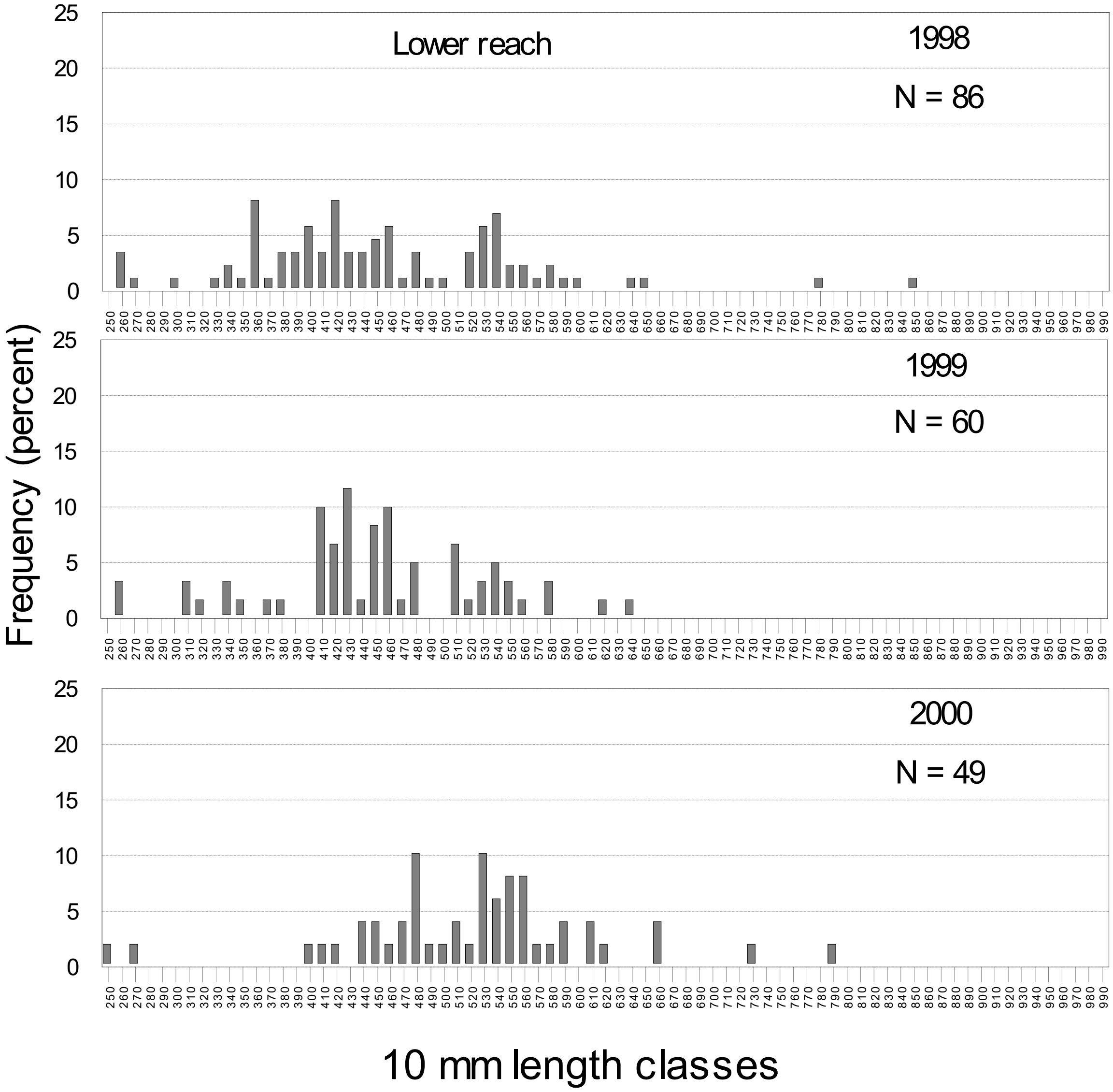


Figure 15. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 1998–2000

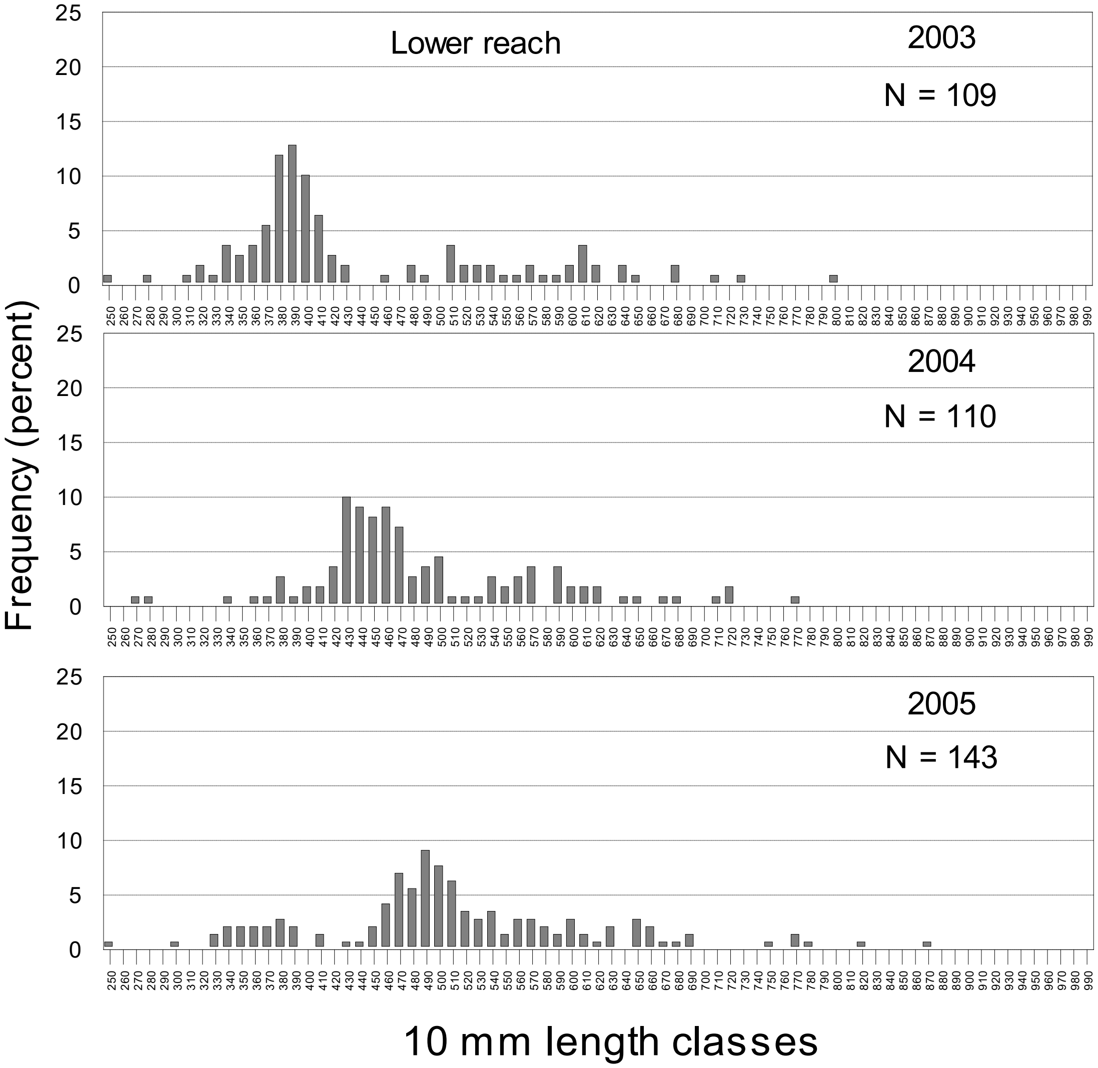


Figure 16. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 2003–2005.

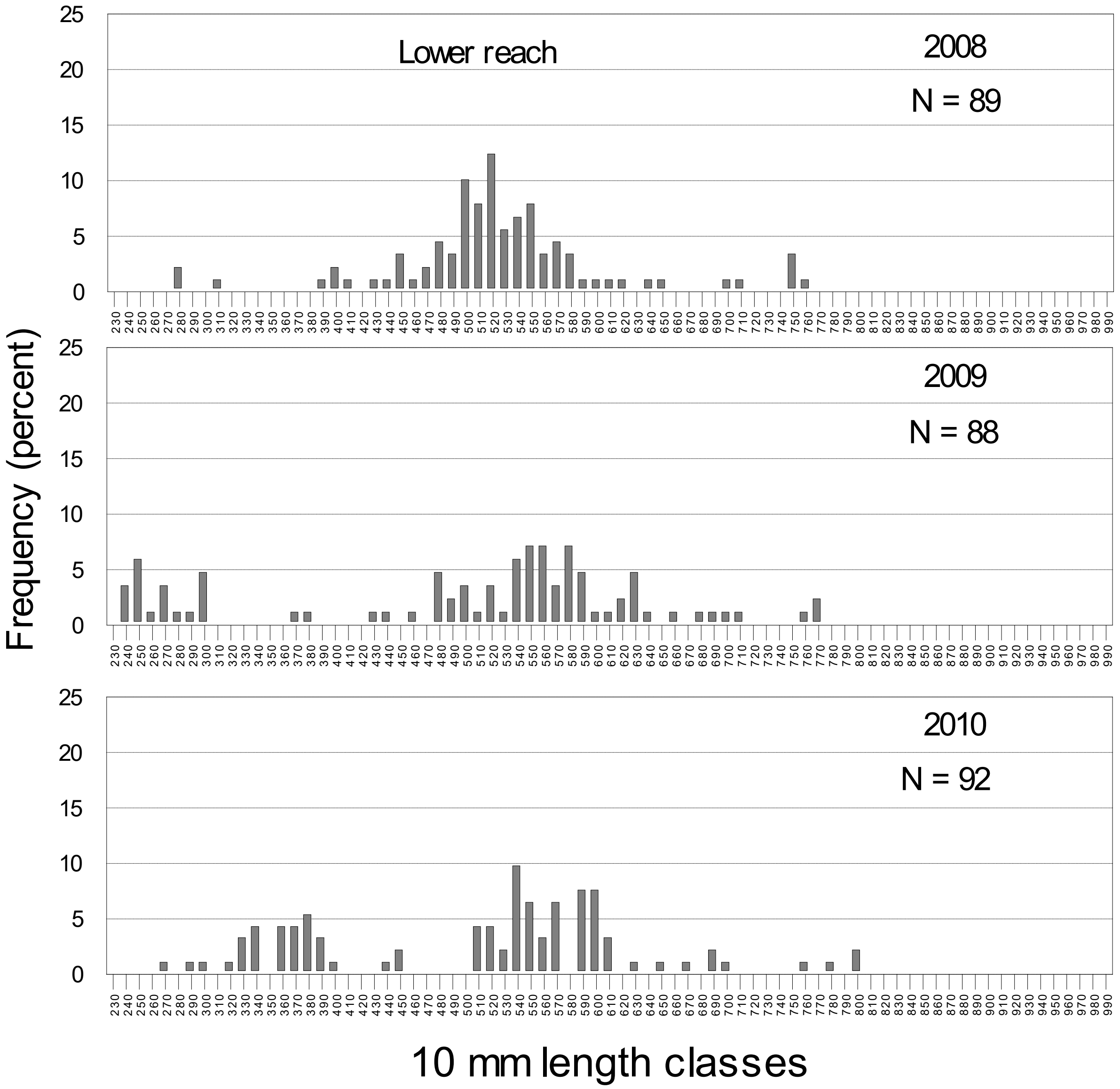


Figure 17. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 2008–2010.

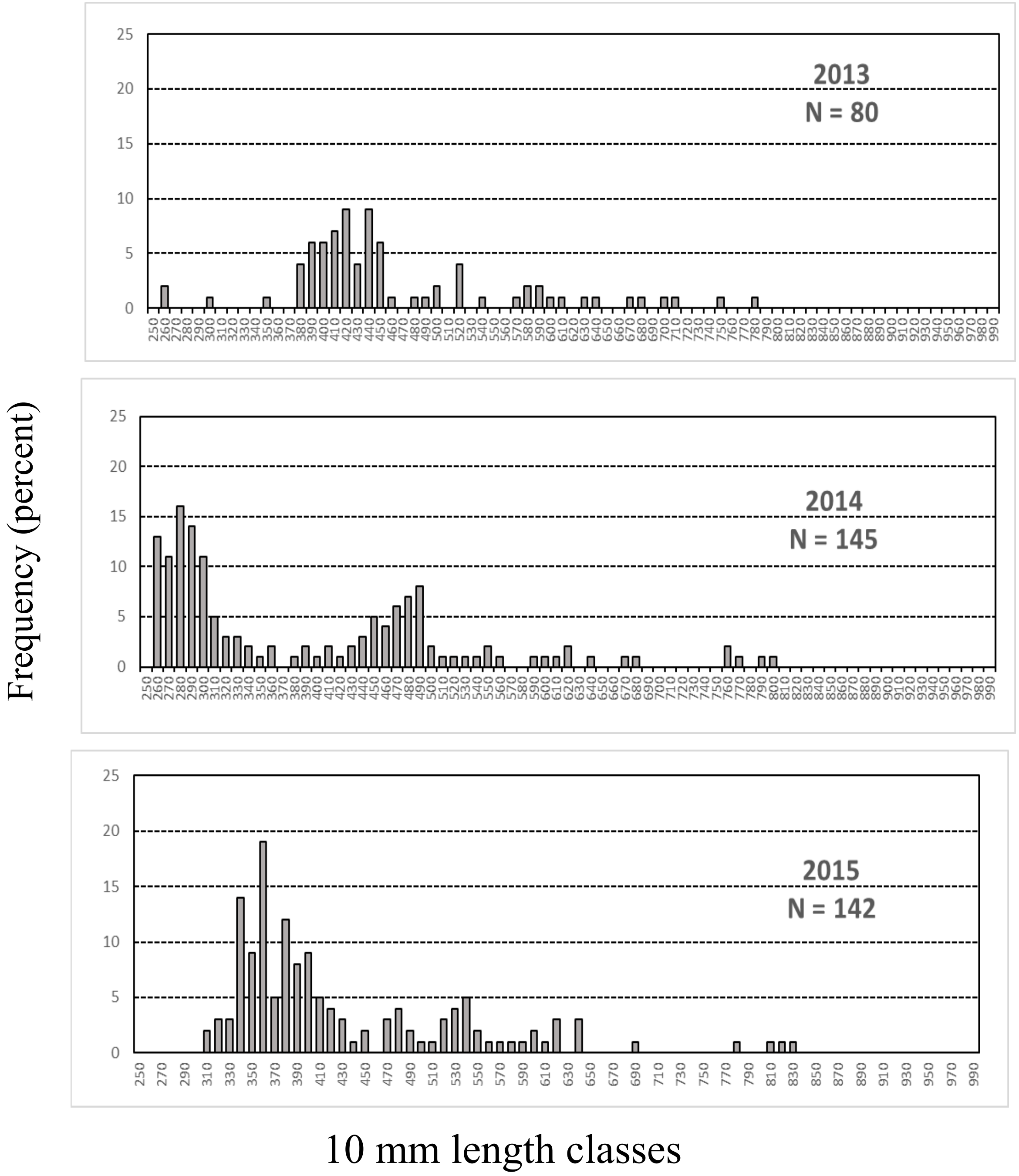


Figure 18. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 2013–2015.

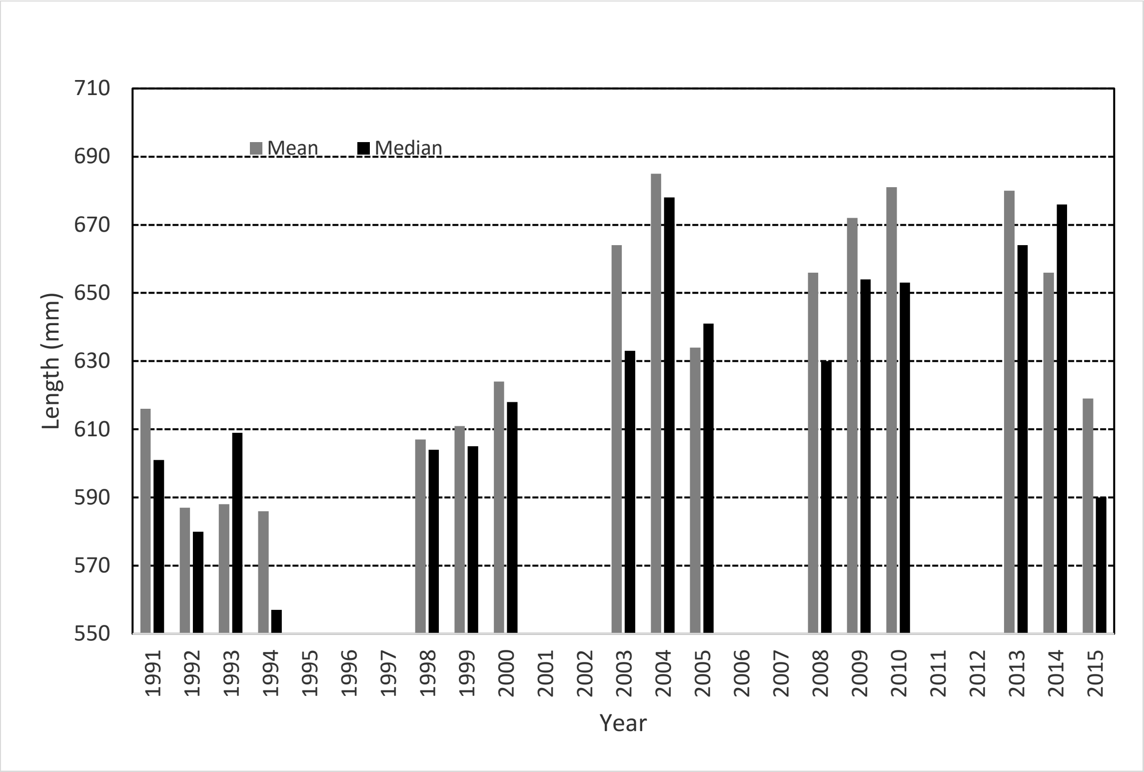


Figure 19. Mean and median lengths of Colorado pikeminnow captured in the upper Colorado River study reach, 1991–2015.

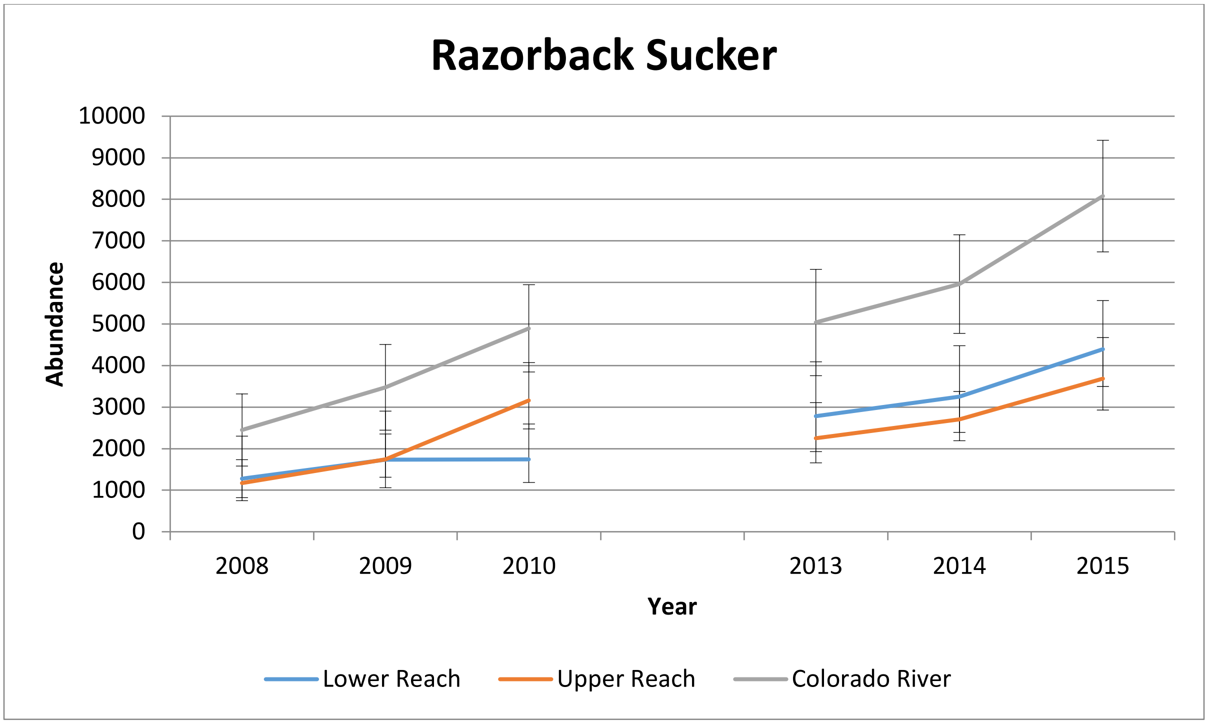


Figure 20. Abundance of razorback sucker in the Colorado River from near Cameo, Colorado downstream to the Colorado/Green Rivers confluence (2008–2010 and 2013–2015). Error bars represent the 95% confidence intervals.

APPENDIX

Appendix Table I. Estimated mean length and mean annual growth increments by age for Colorado pikeminnow in the Colorado River for ages 0–7. Mean length for age 0 value is from Snyder (1981). Mean length at age 1 is from measured lengths of fish seined near RM 54 on June 28, 1989 and assumed to be 1-yr old. Mean lengths of ages 2–7 are from measurements of fish aged using scales. Insufficient captures of age 2 fish precluded estimates of growth increments between ages 1 and 2, and 2 and 3. Growth increments for fish between ages 7 and 8 were not calculated because presumptive age 8 fish could not be reliably aged. Table and caption from Osmundson et al. (1997).

Age (years)	*N*	Total length (mm)			Growth period (age)	Annual growth increment (mm)	
		Mean	Range	SD		Mean	SD
0	8	7.7	7.0–8.5	0.5	0–1	63.5	13.6
1	73	71.2	50–103	13.6	1–2		
2	1	181.0			2–3		
3	3	232.7	190–259	37.3	3–4	82.0	56.0
4	6	314.7	267–374	41.8	4–5	61.5	53.4
5	19	376.2	326–453	33.3	5–6	47.9	45.3
6	10	424.1	375–472	30.6	6–7	32.2	36.6
7	7	456.3	430–479	20.0			

Appendix Table II. Estimated probability of capture ($\hat{p}$) for Colorado pikeminnow in the upper and lower Colorado River study reaches, 1991–2015. Probabilities are presented for secondary (passes) capture occasions.

	Length	Upper Reach Passes					Lower Reach Passes				
Year	(mm)	1	2	3	4	5	1	2	3	4	5
1991	500	0.087	0.067	0.099	--	--	--	--	--	--	--
1992	500	0.061	0.07	0.067	--	--	0.045	0.037	--	--	--
1993	500	0.104	0.108	0.115	--	--	0.091	0.073	--	--	--
1994	500	0.066	0.088	0.09	--	--	0.104	0.049	--	--	--
1998	500	0.091	0.143	0.107	--	--	0.087	0.170	--	--	--
1999	500	0.105	0.132	0.109	--	--	0.100	0.065	--	--	--
2000	500	0.105	0.107	0.057	--	--	0.068	0.039	--	--	--
2003	500	0.027	0.037	0.039	0.027	--	0.011	0.017	0.043	0.041	--
2004	500	0.047	0.04	0.119		--	0.043	0.055	0.043	--	--
2005	500	0.053	0.074	0.062	0.111	0.089	0.042	0.080	0.075	0.058	0.056
2008	500	0.043	0.041	0.046	0.054	0.046	0.037	0.082	0.099	0.065	--
2009	500	0.039	0.046	0.124	0.058	0.096	0.030	0.094	0.082	0.058	--
2010	500	0.058	0.075	0.063	0.088	0.079	0.056	0.041	0.095	0.115	--
2013	500	0.074	0.054	0.059	0.106	0.074	0.039	0.071	0.066	--	--
2014	500	0.063	0.092	0.077	0.101	0.083	0.049	0.064	0.017	0.037	--
2015	500	0.045	0.072	0.072	0.067	0.070	0.047	0.064	0.063	0.043	--
Mean		**0.067**	**0.078**	**0.082**	**0.077**	**0.077**	**0.057**	**0.067**	**0.065**	**0.059**	**0.056**
SE		0.006	0.008	0.007	0.010	0.006	0.007	0.009	0.009	0.01	--

Appendix Table III. Abundance estimates ($\hat{N}$) for Colorado pikeminnow $\geq$ 250 mm TL in the lower and upper Colorado River study reaches, and for the reaches combined, with lower and upper 95% confidence intervals (CI) and standard error (SE). M_{t+1} is the number of unique individuals captured. CV is the coefficient of variation (100 x SE/ $\hat{N}$).

Year	$\hat{N}$	Lower CI	Upper CI	SE	M_{t+1}	CV
			Lower reach			
1992	480.1	151.4	1,714.2	340.4	32	70.9
1993	590.1	314.1	1,203.4	213.2	88	36.1
1994	467.6	265.1	876.0	148.5	66	31.8
1998	402.2	233.2	765.2	128.2	86	31.9
1999	416.1	249.0	731.0	118.2	60	28.4
2000	487.9	275.4	901.5	152.9	51	31.3
2003	1,192.2	683.0	2,155.3	360.8	112	30.3
2004	687.1	445.1	1,093.6	161.1	89	23.4
2005	603.7	456.1	826.3	92.9	166	15.4
2008	347.7	248.0	509.9	65.3	89	18.8
2009	331.9	237.0	484.3	61.7	80	18.6
2010	333.8	247.0	469.2	55.6	92	16.7
2013	448.4	275.9	768.1	120.9	74	27.0
2014	919.6	620.3	1406.8	195.9	144	21.3
2015	705.7	518.4	985.6	117.3	140	16.6
			Upper reach			
1991	217.3	122.7	452.5	77.7	59	35.8
1992	292.4	187.3	487.2	73.7	64	25.2
1993	223.7	167.4	315.6	36.9	78	16.5
1994	370.1	273.5	518.7	61.4	94	16.6
1998	425.5	343.1	543.3	50.4	151	11.8
1999	394.8	323.3	495.0	43.3	145	11.0
2000	377.2	297.8	491.4	48.7	117	12.9
2003	324.7	215.6	505.7	72.1	50	22.2
2004	304.8	221.3	435.1	53.5	72	17.5

2005	416.2	325.1	552.3	57.0	140	13.7
2008	376.3	267.7	548.4	70.2	80	18.7
2009	269.7	199.9	349.7	37.6	81	14.5
2010	248.5	191.4	334.6	35.9	79	14.4
2013	201.1	147.6	287.1	34.8	60	17.3
2014	196.4	149.4	270.7	30.3	69	15.4
2015	219.7	159.7	314.4	38.6	62	17.6
			Combined			
1992	772.5	357.5	1,814.5	348.3	96	45.1
1993	813.9	511.0	1,393.4	213.8	166	26.3
1994	837.7	596.1	1,213.1	154.4	160	18.4
1998	827.7	614.3	1,161.8	136.9	237	16.5
1999	810.9	609.7	1,112.2	126.1	205	15.6
2000	865.1	617.2	1,249.8	158.3	168	18.3
2003	1,516.9	967.0	2,442.3	366.3	162	24.1
2004	991.9	721.4	1,392.9	168.6	161	17.0
2005	1019.2	836.7	1266.4	108.6	306	10.7
2008	724.0	566.4	944.1	95.3	169	13.2
2009	591.7	472.2	757.0	71.9	161	12.2
2010	582.3	472.2	732.7	65.8	171	11.3
2013	649.4	455.8	959.6	125.7	134	19.4
2014	1115.9	803.4	1593.9	198.0	213	17.7
2015	924.7	721.6	1207.52	122.5	202	13.2

Appendix Table IV. Abundance estimates ($\hat{N}$) for Colorado pikeminnow ≥ 450 mm TL in the lower and upper Colorado River study reaches, and for the reaches combined, with lower and upper 95% confidence intervals (CI) and standard error (SE). M_{t+1} is the number of unique individuals captured. CV is the coefficient of variation (100 x SE/ $\hat{N}$).

Year	$\hat{N}$	Lower CI	Upper CI	SE	M_{t+1}	CV
			Lower reach			
1992	159.8	48.1	617.4	121.7	12	76.1
1993	491.7	261.0	1,008.8	179.1	75	36.4
1994	317.2	179.5	599.0	101.8	48	32.1
1998	173.6	99.8	341.6	57.8	42	33.3
1999	205.7	119.6	376.2	62.5	32	30.4
2000	400.4	225.1	745.5	126.9	44	31.7
2003	336.6	182.1	657.8	115.1	39	34.2
2004	388.2	245.3	638.0	97.1	54	25.0
2005	486.3	365.3	670.6	76.5	134	15.7
2008	308.3	218.9	454.8	58.7	79	19.1
2009	252.1	177.7	373.9	48.9	61	19.4
2010	227.6	165.5	327.4	40.4	63	17.7
2013	156.4	91.0	287.6	47.8	26	30.6
2014	297.2	191.8	479.3	71.2	47	24.0
2015	220.0	154.9	335.6	44.6	44	20.3
			Upper reach			
1991	202.3	114.6	421.2	72.2	56	35.7
1992	280.2	179.5	467.2	70.7	62	25.2
1993	212.9	159.2	300.7	35.2	75	16.5
1994	370.2	273.6	518.8	61.4	94	16.6
1998	409.6	330.5	522.7	48.4	147	11.8
1999	383.8	314.4	481.0	42.0	141	11.0
2000	372.7	294.3	485.6	48.2	116	12.9
2003	324.8	215.6	505.8	72.1	50	22.2

2004	299.3	217.3	427.7	52.6	72	17.6
2005	410.2	320.2	544.5	56.3	138	13.7
2008	376.3	267.5	548.5	70.2	79	18.7
2009	259.7	199.9	349.7	37.6	81	14.5
2010	248.5	191.4	334.5	35.9	78	14.4
2013	175.8	127.8	254.1	31.4	52	17.9
2014	185.0	140.3	256.0	28.9	65	15.6
2015	208.5	151.7	300.1	37.0	59	17.8
			Combined			
1992	440.0	250.8	831.9	140.7	74	32.0
1993	704.6	448.3	1,181.3	180.0	150	25.5
1994	687.4	508.1	954.5	112.1	142	16.3
1998	583.1	461.9	758.3	74.6	189	12.8
1999	589.4	466.4	764.1	75.0	173	12.7
2000	773.1	562.3	1,094.6	133.4	160	17.3
2003	661.4	452.4	990.4	134.4	89	20.3
2004	687.6	510.8	945.6	109.3	126	15.9
2005	896.5	736.8	1111.1	94.6	272	10.6
2008	684.5	534.2	895.0	91.0	158	13.3
2009	511.8	409.8	652.7	61.3	142	12.0
2010	476.2	386.3	599.0	53.7	141	11.3
2013	332.2	242.5	470.8	57.1	78	17.2
2014	482.1	359.7	665.0	76.6	112	15.9
2015	428.5	334.2	561.3	57.3	103	13.4

Appendix Table V. Abundance estimates ($\hat{N}$) for Colorado pikeminnow ≥ 500 mm TL in the lower and upper Colorado River study reaches, and for the reaches combined, with lower and upper confidence 95% intervals (CI) and standard error (SE). M_{t+1} is the number of unique individuals captured. CV is the coefficient of variation (100 x SE/ $\hat{N}$).

Year	$\hat{N}$	Lower CI	Upper CI	SE	M_{t+1}	CV
			Lower reach			
1992	75.4	19.9	354.1	68.3	6	90.5
1993	227.8	115.2	500.1	91.1	36	40.0
1994	239.9	133.2	464.8	80.1	37	33.4
1998	111.4	61.1	238.2	41.6	28	37.4
1999	103.7	54.0	220.1	39.5	17	38.1
2000	290.4	159.6	556.5	96.4	33	33.2
2003	297.4	157.0	599.5	106.6	35	35.8
2004	197.3	112.3	368.7	62.3	29	31.6
2005	315.1	233.0	443.4	52.6	87	16.7
2008	261.2	184.2	389.0	50.9	67	19.5
2009	223.0	156.1	333.7	44.2	54	19.8
2010	220.4	159.9	317.7	39.3	61	17.9
2013	126.1	72.0	237.7	40.2	21	31.9
2014	125.8	75.1	223.3	36.3	20	28.8
2015	164.7	115.8	263.9	36.0	33	21.8
			Upper reach			
1991	184.7	104.6	384.6	65.9	51	35.7
1992	258.5	165.4	432.4	65.5	58	25.4
1993	175.1	130.3	249.8	29.7	63	17.0
1994	312.7	230.2	440.6	52.6	80	16.8
1998	393.1	317.0	502.3	46.7	142	11.9
1999	351.5	287.5	441.9	38.9	131	11.1
2000	356.8	281.3	465.4	46.3	110	13.0
2003	324.8	215.6	505.8	72.1	50	22.2

2004	283.6	205.5	406.0	50.1	68	17.7
2005	353.2	274.6	471.4	49.4	119	14.0
2008	376.3	267.3	548.3	70.2	79	18.7
2009	253.4	194.8	341.7	36.8	79	14.5
2010	248.5	191.4	334.5	35.9	78	14.4
2013	169.5	122.9	245.9	30.6	50	18.1
2014	150.8	113.2	212.1	24.6	53	16.3
2015	168.4	121.2	246.1	31.1	48	18.5
			Combined			
1992	334.0	202.0	592.0	95.2	64	28.5
1993	402.9	266.2	651.1	94.8	99	23.5
1994	552.6	407.3	770.7	91.2	117	16.5
1998	504.5	402.7	650.9	62.5	170	12.4
1999	455.3	363.4	586.2	56.1	148	12.3
2000	647.2	479.6	898.2	105.0	143	16.2
2003	622.2	424.7	934.5	127.3	85	20.5
2004	480.9	353.5	671.4	79.8	97	16.6
2005	668.2	547.3	832.0	71.9	206	10.8
2008	637.5	495.4	837.5	86.2	146	13.5
2009	476.4	381.2	608.0	57.2	133	12.0
2010	468.9	380.3	590.0	53.0	139	11.3
2013	295.6	216.4	417.9	50.4	71	17.1
2014	276.6	207.2	381.9	43.8	73	15.8
2015	333.1	256.4	443.5	47.1	81	14.1

Appendix Table VI. Abundance estimates ($\hat{N}$) for Colorado pikeminnow 400–449 mm TL in the lower and upper Colorado River study reaches, and for the reaches combined, with lower and upper 95% confidence intervals (CI) and standard error (SE). M_{t+1} is the number of unique individuals captured. CV is the coefficient of variation (100 x SE/ $\hat{N}$).

Year	$\hat{N}$	Lower CI	Upper CI	SE	M_{t+1}	CV
			Lower reach			
1992	230.1	70.0	856.6	169.8	15	73.8
1993	75.5	27.1	261.6	50.8	10	67.3
1994	48.0	15.9	184.5	35.7	6	74.5
1998	101.9	52.6	228.3	41.2	21	40.4
1999	132.4	70.0	269.7	47.9	18	36.2
2000	56.6	18.2	206.6	40.7	5	71.8
2003	248.5	119.7	549.2	102.2	23	41.1
2004	232.1	132.3	426.5	71.8	27	31.0
2005	25.6	14.6	52.6	9.0	7	35.2
2008	23.6	12.7	52.1	9.2	6	39.0
2009	8.3	3.5	28.5	5.3	2	63.7
2010	7.3	3.2	24.6	4.5	2	61.2
2013	176.2	103.2	321.0	53.1	29	30.1
2014	76.4	42.7	147.1	25.2	12	33.1
2015	85.7	51.8	142.4	22.5	17	26.3
			Upper reach			
1991	10.1	2.8	84.3	14.1	2	140.3
1992	6.9	1.3	114.9	17.5	1	252.7
1993	11.6	4.0	79.9	13.6	3	116.9
1994	1.2	0.0	129.5	20.7	0	1,721.8
1998	12.1	3.5	162.4	24.8	3	204.8
1999	8.3	3.2	160.4	2,301	3	277.0

2000	5.8	1.2	153.1	22.2	1	382.6
2003	1.1	0.0	124.3	20.2	0	1,851.3
2004	6.5	1.3	122.8	18.4	1	281.5
2005	3.0	1.3	14.3	2.5	1	82.9
2008	0.0	0.0	0.0	0.0	0	N/A
2009	0.0	0.0	0.0	0.0	0	N/A
2010	0.0	0.0	0.0	0.0	0	N/A
2013	22.1	12.9	45.4	7.6	7	34.5
2014	8.5	4.5	23.4	4.1	3	48.4
2015	3.5	1.4	17	3.0	1	86.0
			Combined			
1992	237.0	73.2	869.7	172.4	16	72.7
1993	87.1	31.4	311.9	60.2	13	69.1
1994	49.2	12.6	287.3	52.8	6	107.4
1998	114.1	53.2	302.1	56.4	24	49.4
1999	140.7	68.4	323.2	59.9	21	42.5
2000	62.4	16.7	302.6	57.8	6	92.5
2003	249.6	113.1	593.0	112.8	23	45.2
2004	238.6	130.2	461.8	80.4	28	33.7
2005	28.6	16.8	56.0	9.3	68	32.3
2008	23.6	12.7	52.1	9.2	56	39.0
2009	8.3	3.5	28.5	5.3	2	63.7
2010	7.3	3.2	24.6	4.5	2	61.9
2013	198.2	122.3	340.9	53.6	36	27.0
2014	84.9	49.9	155.0	25.6	15	30.1
2015	89.2	56.7	149.1	22.7	18	25.5

Appendix Table VII. Abundance estimates ($\hat{N}$) for razorback sucker in the lower and upper Colorado River study reaches, and for the reaches combined, with lower and upper 95% confidence intervals (CI) and standard error (SE). M_{t+1} is the number of unique individuals captured. CV is the coefficient of variation (100 x SE/ $\hat{N}$).

Year	$\hat{N}$	Lower CI	Upper CI	SE	M_{t+1}	CV
			Lower reach			
2008	1277.7	747.5	2300.6	379.7	177	29.7
2009	1732.9	1059.7	2902.8	456.1	147	26.3
2010	1738.6	1185.9	2593.3	352.2	175	20.3
2013	2784.2	1927.4	4089.6	541.9	291	19.5
2014	3255.1	2391.0	4477.0	525.7	304	16.2
2015	4393.3	3495.9	5563.7	523.7	546	11.9
			Upper reach			
2008	1171.4	820.3	1734.2	228.0	238	19.5
2009	1742.7	1312.3	2352.6	262.1	280	15.0
2010	3156.5	2474.6	4070.2	403.5	469	12.8
2013	2251.0	1658.7	3106.7	364.4	326	16.2
2014	2705.0	2190.4	3375.5	300.1	495	11.1
2015	3684.7	2929.4	4673.3	441.6	483	12.0
			Combined			
2008	2449.1	1581.0	3317.1	442.9	415	18.1
2009	3475.6	2444.5	4506.8	526.1	427	15.1
2010	4895.0	3845.2	5944.9	535.6	644	10.9
2013	5035.2	3755.3	6315.1	653.0	617	13.0
2014	5960.2	4773.6	7146.7	605.4	799	10.2
2015	8078.0	6735.3	9420.8	685.1	1029	8.5