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Population Structure, Abundance and Recruitment of Colorado Pikeminnow of the Upper Colorado River, 1991-2010

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Final Report

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Prepared by

Douglas B. Osmundson[1] and Gary C. White[2]

[1]*Colorado River Fishery Project, U. S. Fish and Wildlife Service, 445 West Gunnison Ave., Suite 140,*
Grand Junction, Colorado 81501, USA

[2]*Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins 80523, USA*

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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 2010 were used to assess population trends of Colorado pikeminnow *Ptychocheilus lucius* in the upper Colorado River. Four multi-year data collection efforts were made: 1991–1994, 1998–2000, 2003–2005, and 2008–2010. Primary objectives included capturing and marking Colorado pikeminnow $\geq$ 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 three study periods have been provided in previous reports, we provide here a synthesis of those results with those from the most recent study period, 2008–2010.

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, and (2) the upper reach, extending from Westwater Wash 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 spring runoff of the first two multi-year sampling periods, the upper reach was sampled three times; the lower reach, two times. Backwater trammel netting was the primary means of sampling, supplemented with shoreline boat electrofishing. In most cases, one two-person crew did all the sampling. In the most recent two multi-year sampling efforts, four two-person crews worked concurrently: two in the upper reach; two in the lower reach. Most of the recent sampling was done with electrofishing. Depending on the duration of runoff, three to five passes through each reach were made each year. In all sampling periods, captured Colorado pikeminnow were measured, weighed, PIT-tagged and released.

For the 1991–2005 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, 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. Because there was a change in PIT tag type and reader technology in 2004, new readers could not read early tags and were therefore incapable of detecting recaptures in some previously tagged fish. For 2004 and 2005, both reader types were used to look for old and new tags and only new-type tags were implanted in newly captured fish. In addition, captured Colorado pikeminnow containing an old type tag were also implanted with a new tag. A new capture history matrix was developed using only capture data from individuals tagged with the new tag type and included years 2004–2010. Probably because this data set was smaller, in both years and total number of fish, the top model included a reach effect on survival, but no fish length or time effect.

Twelve combined-reach annual abundance estimates and one earlier (1991) upper-reach estimate indicated the Colorado River population increased substantially in number from 1991 through 2005. Combined-reach point estimates of individuals ≥ 450 mm TL increased from 440 in 1992 to 889 in 2005. However, abundance estimates significantly declined between 2005 and 2009. Probability of capture varied among years and was generally lowest during the most recent three-year period despite additional effort expended. During 2008–2010, lower-reach fish had higher capture probabilities than upper-reach fish. Survival also varied by reach: fish in the upper reach had a significantly higher survival rate (88.4%) than fish in the lower reach (72.7%). Overall annual survival rates (combined-reach estimates) for fish ≥ 500 mm TL appeared to decline over time from 88% (1991–1994) to 86% (1998–2000) to 80% (2003–2005). However, because there was no fish length effect found using the recent data, survival rates were calculated for all fish ≥ 250 mm TL for years 2008–2010 and comparisons with the earlier rates could therefore not be made.

Annual recruitment (number of fish 400–449 mm TL) appeared to exceed the estimated number of annual mortalities of fish ≥ 450 mm TL in six of the 12 years for which estimates were available. The estimated net gain for the 12 years studied was 32 fish ≥ 450 mm TL. Because estimates were not available for 1995–1997, 2001–2002, and 2006–2007, total gain or loss for the 19-year period could not be estimated. However, even with very rough estimates and with seven years of data missing, the gain reported is generally supported by the combined-reach population estimates for fish $\geq$ 450 mm TL: $\hat{N}$ = 440 in 1992 and $\hat{N}$ = 493 in 2010. A weighted regression analysis of abundance estimates lent support to the trend of an increasing population in the upper reach followed by a later decline. For the lower reach, and the study area as a whole, weighted regression indicated a stable population over the length of the study period. This was despite a significant decline in adult abundance from 2005 to 2009-2010.

Precision of estimates affects the ability to detect change in population abundance over time. Precision of abundance estimates as measured by the coefficient of variation (CV; a smaller number has higher precision) was lowest during the first multi-year effort (mean CV of 24%), higher during the second and third multi-year efforts (mean CVs of 14% and 15%, respectively), and highest in the most recent period (mean CV of 13%).

Electrofishing catch rates (mean number of Colorado pikeminnow captured per hour), used in the past (Interagency Standardized Monitoring Program; ISMP) as a means to detect trends in population abundance and as a consistency check for mark-recapture estimates, did not track trends in mark-recapture abundance estimates when all years were included (1986-2005). When electrofishing catch rates were compared with abundance estimates for only those recent years with consistent gear and protocol (2003-2005 and 2008- 2010), the two indices tracked each other relatively well.

A qualitative assessment of year-class strength, based on relative abundance of age-5 fish (326-453 mm long) in annual length-frequency histograms from the lower reach, suggested there were 12 weak year-classes, six year classes of moderate strength, and only two strong ones in the 20 years from 1986 to 2005. A comparison of annual catch rates of young-of-the-year Colorado pikeminnow in fall seine surveys (from ISMP studies) in the lower reach with later strength of the corresponding year-class at age-5 indicated that relative abundance in fall of the first year of life is a poor predictor of later recruitment strength. First-year, over-winter mortality and perhaps runoff conditions the following spring might contribute to annual variation in cohort survival rates, but environmental factors influencing survival then and during the subsequent four years of life remain largely unknown.

No relation was found between annual abundance estimates and mean body condition of adult Colorado pikeminnow. In the upper reach, regression of abundance point estimates of Colorado pikeminnow $\geq$ 500 mm TL with mean condition factor (*Kn*) indicated a negative but weak and non-significant relationship (as abundance went up, condition declined). For the lower reach sub-population, regression indicated a positive, but weak and non-significant relationship between the two variables (as abundance increased, body condition improved). In addition, in both reaches, mean *Kn* was not significantly lower in 2005 (the year with the highest abundance estimate) than in 2010, a year when the river-wide abundance estimate was significantly lower than in 2005. Hence, there was no body condition evidence to suggest that food was limiting during the year when abundance was highest ($\hat{N}$ = 889 for fish > 450 mm TL).

The Recovery Program's database of PIT-tagged Colorado pikeminnow captured from throughout the Colorado and Green river sub-basins revealed that 54 individuals, or 1.8% of the total number of fish recaptured at least once (2,976), moved between the Colorado River and Green River systems between 1990 and 2010. As reported previously, this level of movement suggests enough gene flow to keep the two populations from genetically differentiating over time but not enough exchange of individuals for one population to affect the demographics of the other population.

Although the Colorado River population of Colorado pikeminnow remains self-sustaining, the recent decline in abundance is cause for concern. Recruitment strength in recent years has been weak and not kept pace with adult mortality. Additionally, adult mortality may be trending higher in the lower reach. Results of sampling beginning in 2013 will indicate whether we can expect any strong or moderately strong year classes in the near future that might allow sufficient recruitment to arrest or reverse recent declines in adult abundance.

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. We recommend the current sampling regime be continued.

INTRODUCTION

Colorado pikeminnow *Ptychocheilus lucius* Girard once ranged throughout warm-water reaches of the Colorado River Basin, from the Wyoming border south to the Gulf of California. Today, the species is 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 and two primary tributaries, the White and Yampa rivers, and also in some smaller tributaries such as the Duchesne, Price and San Rafael rivers. Abundance in that sub-basin was estimated at 3,656 adults in 2008, not counting the few that may have resided in the smaller tributaries (Bestgen et al. (2010). A few wild individuals may still persist in the San Juan River, a Colorado River tributary that today flows directly into Lake Powell. That population 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 of that population is 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 multi-year, mark-recapture field effort conducted during 2003–2005 were reported by Osmundson and White (2009). Results from the most recent effort (2008–2010) are provided here along with a synthesis of results for the entire 1991–2010 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 late juvenile and adult Colorado pikeminnow, and other endangered fishes when encountered, while making four 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) and the Colorado Parks and Wildlife (CPW). 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 there. Hence, 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). However, all fish moving upstream through the ladder were first captured in a fish trap, sorted and identified before release. Hence, 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. Hence, such 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

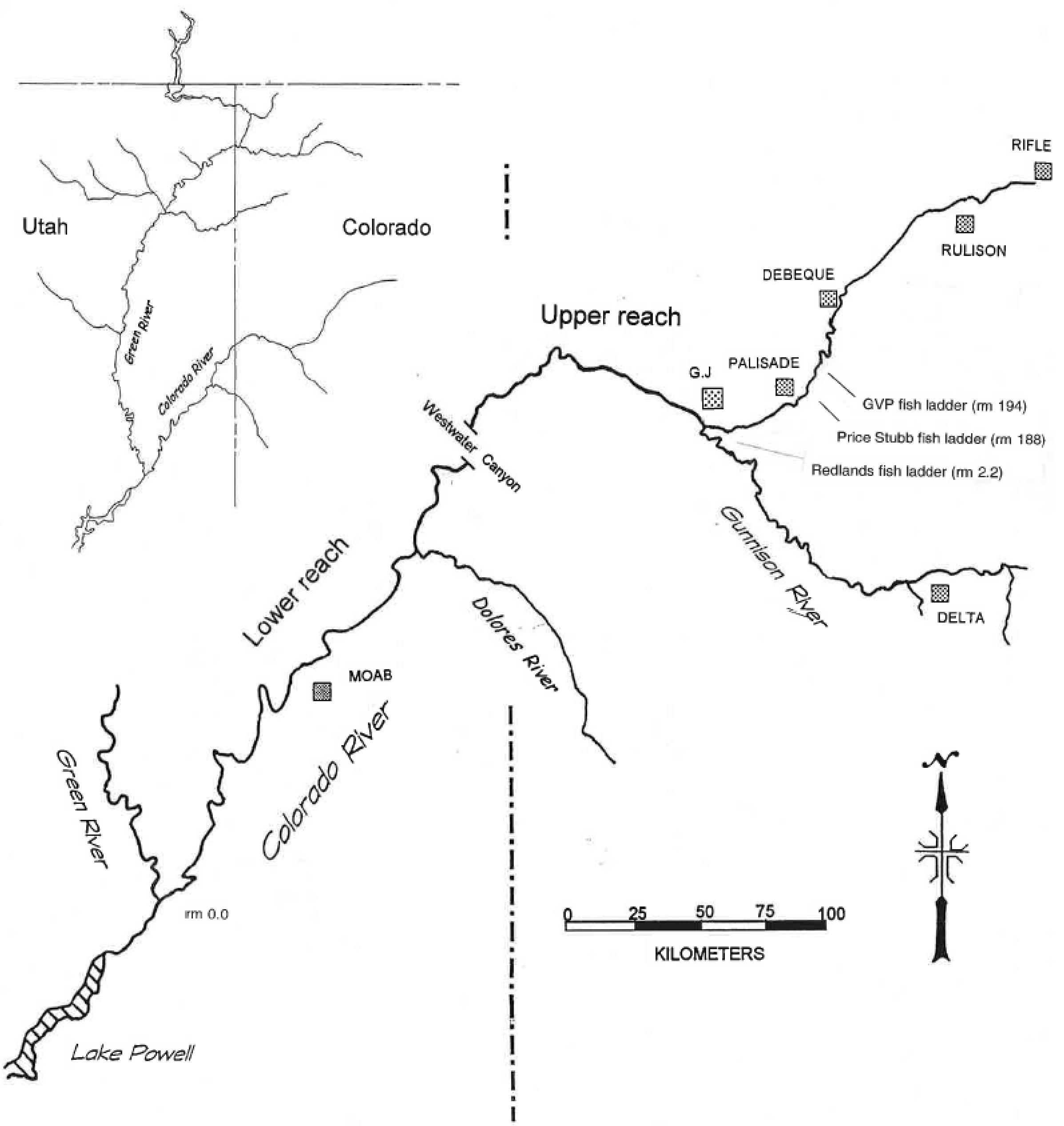

Figure 1. Map of the upper and lower reaches of the Colorado River study area. The downstream boundary of the lower reach was the confluence with the Green River (river mile [rm] 0.0) and the upstream boundary was the lower end of Westwater Canyon (rm 112). The downstream boundary of the upper reach was the upper end of Westwater Canyon (rm 124) and the upstream boundaries were the fish ladders at rm 188 (1991-2005) and rm 193.7 (2008-2010; 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 GVP.

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). 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 the limit of the fish's range at Palisade, Colorado, where the Price Stubb Dam (RM 188.3), built in 1911, blocked further upstream fish movement. In early 2008, the dam was removed and a fish ladder was built on one side of the channel 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 (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 only during the recent 2008–2010 period.

Fish Capture and Marking

Capture methods during the 2008–2010 effort essentially followed those of the earlier three multi-year efforts, previously described in the aforementioned reports (Osmundson and Burnham 1998, Osmundson 2002, Osmundson and White 2009). Those procedures common to all four 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 Colorado pikeminnow $\geq$ 250 millimeters (mm) long during early- or mid-April to mid-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 reaches where, or at times when, backwaters were few.

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 set inside the backwater. The total number of nets set (1–5) increased with backwater size. A 4.3-m-long motorized aluminum jonboat 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. 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, ensnared Colorado pikeminnow were placed in a live well until all fish were removed from all nets. The net set at the backwater mouth was always pulled last. 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 two 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. With each pass, every backwater deep enough to allow entry by the 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. Both 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 the 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 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, electrofishing only was employed.

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. In fact, no trammel-netting was done in 2004. Increased runoff in 2005, 2008, 2009, and 2010 allowed more backwater netting. When conditions allowed netting, 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 on where the operator perceived the best habitat to be. 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 nine days to complete in the upper reach and 11 days in the lower reach. In contrast to the first two sampling periods, electrofishing was done throughout the upper and lower reaches during the latter two sampling periods.

The goal during the latter two multi-year, sampling periods was to complete 4-5 passes annually. However, because of vagaries of the runoff season, the annual 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.

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). Those individuals that were last detected moving upstream of the Redlands Fish Ladder, were designated as ’removed’ and zeros in subsequent passes of the capture history matrix were therefore ignored in the likelihood calculation so that mortality rate would not be overestimated.

For 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 PIT tags in captured Colorado pikeminnow. For those individuals found to contain an older tag, we re-tagged them with a new tag. So for two years, we had two readers on each boat: one for the old tags and one for the new tags. Over time, the old readers failed and the manufacturing company refused to repair them. Although the new readers can be set to look for the old tag type and then reset to look for the new type, we encountered problems with this. One was that during the first few years of PIT tagging (1991–1993), an early version of the older tags was used, and these could not be read by the new readers. Hence, many early fish in our matrix could not be 'recaptured' in recent years, thereby biasing some aspects of model output. Additionally, we found that field crew members often made mistakes when changing the settings on the new readers to search for the two tag types. With the high turnover rate of seasonal field technicians, we considered the possibility for error too high (i.e., failing to detect existing tags in fish because of improper reader settings). However, we needed to detect old tags in stocked razorback sucker (*Xyrauchen texanus*) that we encountered, so starting in 2008 the new 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 tags (with the stronger signal) were often detected if both types were present in a fish (i.e., the old type was not always detected).

Because of the uncertainty associated with reliably detecting the old tags with the new 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 or succeeding the years of interest (2008–2010 in this case). Hence, variance associated with the estimate of 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 2004–2010 analysis because of the smaller data set. Transition probabilities from lower to upper reach (ψ^{LU}) and upper to lower reach (ψ^{UL}) were computed for intervals between primary occasions.

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 the individual covariate length was a predictor of capture probability. In our previous analysis (Osmundson and White 2009), we 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 analysis.

Estimates were constructed by using model averaging with model weights from the combined analyses to obtain estimates for four size classes of Colorado pikeminnow: $\geq$ 250 mm TL (essentially all sampled fish), 400–449 mm TL (Recovery Goal length criterion used to define fish about to recruit; USFWS 2002), $\geq$ 450 mm TL (Recovery Goal length criterion used to define adults; USFWS 2002), and $\geq$ 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 be 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. Toward this end, 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 each weight 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. — Annual relative abundance of Colorado pikeminnow, as measured by catch rate (mean number captured per hour of electrofishing), was monitored from 1986 to 2000 by CDOW and UDWR as part of the Interagency Standardized Monitoring Program (ISMP). Because this program was discontinued, electrofishing catch rates during 2003–2005 were computed by Osmundson and White (2009) to extend the long-term catch rate results and to see whether ISMP sampling reaches provided a good representation of river-wide catch rates. No upward trend was indicated when the annual river-wide mean catch rates were regressed as a function of year, even though mark-recapture-based population estimates from 1992 to 2005 clearly indicated an upward trend in population abundance. However, an upward trend in catch rates was indicated when the 2003–2005 non-ISMP results were removed. One possible explanation offered by the authors was that the recent catch-rate results may have been biased low by a change in electrofishing protocol, whereby backwaters were no longer shocked on days when trammel-netting was concurrently conducted. Osmundson and White (2009) concluded that although ISMP sampling reaches did provide good representation of river-wide rates, there were enough dissimilarities in sampling protocol and equipment between ISMP sampling and our recent sampling that results were not comparable and therefore should not be combined with earlier results to deduce trends. With this in mind, we looked (this report) for trends in catch rates using only results from years after the new electrofishing protocol was implemented (i.e., 2003–2005 and 2008–2010). Although time of year (spring) was similar to the earlier ISMP sampling, we used all areas sampled in calculating 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 boat days in all passes. Because mean annual catch rates were non-normally distributed, they were first converted to geometric means before making trend comparisons with abundance point estimates.

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 similar trammel net catch rates for years 2003–2005 and 2008–2010 both for Colorado pikeminnow and sympatric species co-occurring in netted backwaters.

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: 1) 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), and 2) sampling effort in the two reaches was unequal in many years (i.e., more passes in one reach than the other) so fish from the reach with fewer passes would therefore be under represented in a pooled sample. Hence, length frequencies from each reach are presented separately. Prior to presenting the recent length frequencies developed from Colorado pikeminnow captured in 2008–2010, we review those from earlier sampling efforts.

Temporal variation in median 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. 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. — We also used relative abundance at the late juvenile stage as a means to gauge strength of cohorts and estimate the frequency of weak, moderately-strong, and strong recruitment year-classes. As Colorado pikeminnow grow beyond age-5 it becomes progressively difficult to assign age to an individual based on its length. In addition, capturing individuals younger than age-5 appears limited by the gear types used for this study. We therefore used strength 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 (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 (from 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.

Year-class strength at age-5 in relation to strength at age-0. — To test whether year-class strength at age-0 was a good predictor of later strength at age-5, we compared age-5 strength to strength of the corresponding year-class at age-0 as measured from fall young-of-the-year (YOY) seine surveys. Seining age-0 Colorado pikeminnow from backwaters during fall (September-October), when young are 2–4 months old, has been systematically conducted by various researchers from 1982 to the present. Catch rates of YOY Colorado pikeminnow (mean number per area seined) from this fall dataset provide the only available long-term index of age-0 relative abundance in the Colorado River against which the strength of age-5 cohorts can later be compared. Investigators with Utah Division of Wildlife Resources (UDWR) recently presented their summarization of 25 years (1986–2009) of YOY data collected from RM 0–110 by their agency for the Recovery Program's Interagency Standardized Monitoring Program (see Breen et al. 2011). UDWR's 2010 annual report to the Recovery Program (Badame et al. 2010) provided annual YOY catch-per-effort results through 2010.

We assigned each mean annual catch rate of YOY reported by Badame et al. (2010) for 1986–2005 to one of three strength categories for comparison with the corresponding assigned strength category at age-5. Categories for YOY were as follows: Weak: < 2.0 YOY/100 m^2; Moderate: > 2 and < 9 YOY/100 m^2; Strong: > 9 YOY/100 m^2. The non-parametric Fisher Exact Test was used to compare the 20 early year-class strengths with the later strength outcomes at the late juvenile phase (age-5 in most cases) to see if relative strength at age-0 (in fall of the first year) is a useful measure or predictor of later year-class strength as juveniles near the sub-adult stage. The null hypothesis was that the later year-class strength is independent of strength at age-0.

Body condition. — Relative condition was calculated for each Colorado pikeminnow for which there were length and accurate weight measurements (those weighed with an electronic balance). Relative condition accounts for allometric growth and therefore allows condition comparisons among size-classes (Le Cren 1951). Relative condition (K_n) is the observed mass (M_o) of a given fish divided by the expected mass (M_e) for a fish of its length:

$$K_n = \frac{M_0}{M_e} \times 100$$

M_e is calculated using constants derived from mass-length regressions:

$$\log_{10} M_e = ((\log_{10} \text{length}) \text{ slope}) + y\text{-intercept}$$

The constants for these month-specific mass-length regressions were previously derived from Colorado pikeminnow captured from the Colorado River during 1991–1994 and provided in Osmundson et al. (1998). Relative condition of each individual was calculated using the constants specific to the month during which the fish was captured. Mean K_n was then compared between upper and lower reaches within 100-mm length-classes and among length-classes within reaches. To simplify monitoring relative body condition through time, the mean K_n of one length class (500–599 mm TL) was used as an index for making among-year comparisons. This length-class was well suited for this because it occurred in both reaches in all years, sample sizes were relatively large, and because mean K_n of these fish significantly differed in the two reaches in all four sampling periods.

To examine whether body condition might be related to increases in population abundance (i.e., a density-dependent response), we regressed our annual, reach-specific K_n means of fish $\geq$ 500 mm TL (dependent variable) against the annual reach-specific abundance point estimates of fish $\geq$ 500 mm TL (independent variable). Separate regressions were done for upper- and lower-reach groups of fish. Mean K_n from fish $\geq$ 500 mm TL were used in the regressions, rather than from the 500-599 mm length class, so that the same group of fish used in the population estimates were represented in the comparisons.

Inter-system movements. — Movement of marked Colorado pikeminnow between the Colorado and Green River systems was enumerated through inspection of the Colorado pikeminnow PIT-tag database maintained by the Upper Colorado River Endangered Fish Recovery Program. 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, Duschene, Little Snake and Yampa rivers) was previously documented by Osmundson and White (2009) with capture-recapture data through 2005. Here, we update our summarization of such movements using additional data collected from 2006 through 2010.

RESULTS

Fish Captures

There were 398 unique Colorado pikeminnow captured during the recent 2008–2010 study period. The new capture-history matrix, extending back to 2004 and ending with 2010, included 721 unique individuals. The prior matrix (1991–2005) included 1,258 unique fish. The new matrix consisted of 20 lower-reach passes and 23 upper-reach passes. Numbers of captures per pass per reach ranged from 13 to 50 (Table 1). There were 12 fish captured in the first year that were recaptured six years later in the last year of study: two in the lower reach and 10 in the upper reach.

Model Selection

Parameters for the von Bertalanffy growth curve were estimated, with an asymptotic size of 814 mm TL (Table 2). These values were used to predict fish lengths for unobserved fish in the robust-design multi-state model.

Table 1. Total number of Colorado pikeminnow $\geq$ 250 mm TL captured in each sampling pass and year in the Colorado River study area, Colorado and Utah, 2004–2010. 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.

	Lower reach passes					Upper reach passes				
Year	1	2	3	4	5	1	2	3	4	5
2004	28	36 (1)	27 (1)	-	-	19	16 (2)	48 (8)	-	-
2005	26	50 (3)	47 (8)	36 (9)	34 (7)	22	31 (4)	26 (4)	46 (5)	38 (9)
2008	13	29 (1)	27 (3)	23 (7)	-	17	15 (0)	17 (1)	20 (2)	16 (2)
2009	10	31 (0)	27 (3)	19 (4)	-	10	13 (0)	32 (0)	15 (2)	23 (9)
2010	19	13 (1)	32 (3)	38 (3)	-	14	19 (1)	15 (1)	22 (3)	17 (2)

Table 2. Estimates for the von Bertalanffy growth curve for Colorado pikeminnow in the Colorado River study area, 2004–2010. *K* is the von Bertalanffy growth coefficient; L_∞ is the asymptotic length.

Parameter	Estimate	Standard error	95% CI (lower)	95% CI (upper)
K	0.0873	0.00565	0.0761	0.0984
L_∞	813.5	14.7655	784.4	842.6

The minimum AIC$_c$ model {S(reach) ψ(reach*intlen+reach*length) *p*(year*reach*pass)}included a reach effect on survival (*S*), but no fish length (TL) or time effect on *S* (Table 3). Hence, survival is assumed constant across years, but different in the two reaches. The reach + length model was 1.0945 units larger, whereas the reach + year time-specific model was 3.9173 units larger, with neither being supported compared to the reach-only model (Table 3). For the minimum AIC$_c$ model, transitions ψ^{LU} and ψ^{UL} between the two reaches (movements from lower to upper reach and from upper to lower reach) were time-specific in that the transition probabilities were required to be different for 1-year versus 3-year intervals. The transitions ψ^{LU} and ψ^{UL} were also length-specific, and when models with constant transitions were considered, all were completely unsupported with ΔAIC$_c$ > 29. Initial capture probabilities (*p*) were reach- and time-specific for both primary and secondary occasions, but not length-specific. When length for *p* was included as a linear effect in the minimum AIC$_c$ model, the resulting model was 1.9867 units larger than the top model. No other models of *p* were considered because of the differences in *p* within and between primary sessions.

Capture Probability

When the whole study period was considered and fish length held constant (500 mm TL), capture probabilities were highly variable between reaches and within and among primary sessions (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.

Table 3. Model selection results of the robust design multi-state model for Colorado pikeminnow in the upper Colorado River (2004–2010). Abbreviations include: Survival (*S*), reach (reach), transition or movement rates between reaches (ψ), probability of capture (*p*), and fish total length (length). Also considered as covariates in these models were primary and secondary occasion time effects. 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*).

Model	AIC_c	$\Delta\mathrm{AIC}_c$	AIC_c Weights	Model Likelihood	No. Parameters	Deviance
{*S*(reach) ψ(reach*intlen+reach*length) *p*(year*reach*pass)}	5117.54	0.00	0.48	1.00	51	5010.36
{*S*(reach+length) ψ(reach*intlen+reach*length) *p*(year*reach*pass)}	5118.65	1.12	0.27	0.57	52	5009.27
{*S*(reach) ψ(reach*intlen+reach*length) *p*(year*reach*pass+length)}	5119.52	1.99	0.18	0.37	52	5010.13
{*S*(year+reach) ψ(reach*intlen+reach*length) *p*(year*reach*pass)}	5121.45	3.92	0.07	0.14	54	5007.63
{*S*(reach+length) ψ(reach*intlen) *p*(year*reach*pass)}	5147.05	29.52	0.00	0.00	50	5042.07
{*S*(reach+length) ψ(reach*intlen) *p*(year*reach*pass+length)}	5149.22	31.69	0.00	0.00	51	5042.04
{*S*(year+reach+length) ψ(reach*intlen) *p*(year*reach*pass)}	5149.85	32.32	0.00	0.00	53	5038.25
{*S*(year*reach) ψ(year*reach) *p*(year*reach*pass)}	5157.74	40.21	0.00	0.00	59	5032.77
{*S*(year+length) ψ(reach*intlen) *p*(year*reach*pass)}	5161.07	43.54	0.00	0.00	52	5051.69
{*S*(year+reach+length) ψ(reach*intlen) *p*(year*reach)}	5190.03	72.49	0.00	0.00	20	5149.23
{*S*(length^2) ψ(reach*intlen) *p*(year*reach)}	5194.89	77.36	0.00	0.00	17	5160.31
{*S*(length) ψ(reach*intlen) *p*(year*reach)}	5196.95	79.41	0.00	0.00	16	5164.43
{*S*(length) ψ(reach*year) *p*(year*reach)}	5200.48	82.94	0.00	0.00	20	5159.68
{*S*(year+length) ψ(reach*intlen) *p*(year*reach)}	5201.44	83.91	0.00	0.00	19	5162.72

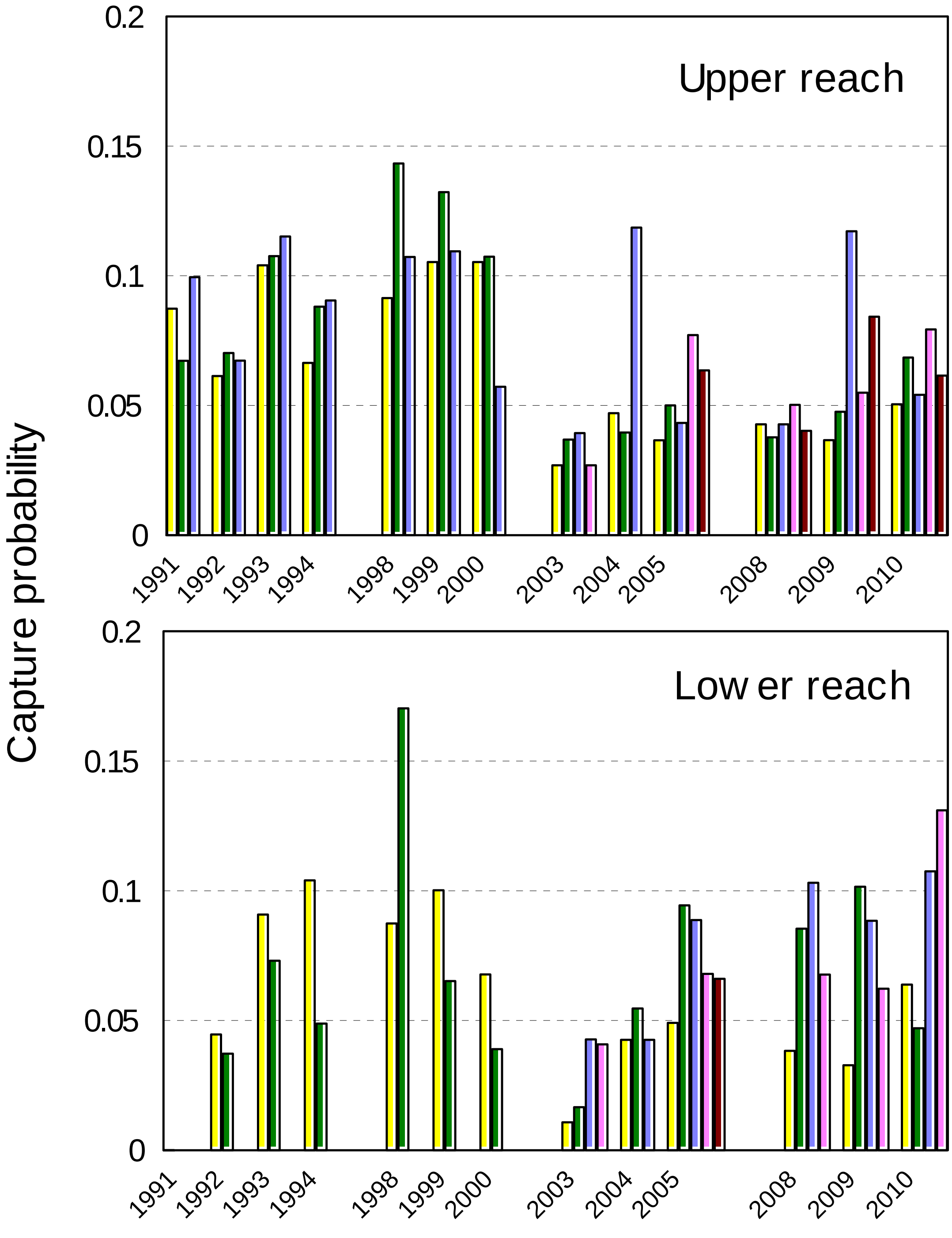

Figure 2. Capture probability by pass in the upper (top panel) and lower (bottom panel) reaches for a Colorado pikeminnow with a length standardized at 500 mm TL. Each bar represents a separate sampling pass. Passes are grouped by year: pass 1: yellow; pass 2: green; pass3: purple; pass 4: magenta; pass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

Capture effort, not considered in calculating capture probability, can bias capture probability. The especially high capture probability in the upper reach during pass 3 of 2004 reflects additional sampling effort in July that was later added to pass 3 (see Figure 2). In other years, effort was fairly similar among passes. During the 2008–2010 sampling period, capture probability during the various passes was generally higher in the lower reach than in the upper reach, with the mean capture probability in the lower reach (mean = 0.077) differing significantly ($P = 0.04$) from that in the upper reach (mean = 0.058). During the previous 3-year sampling effort (2003–2005), capture probability was essentially equal in the upper (mean = 0.050) and lower (mean = 0.051) reaches. In the upper reach, probability of capture clearly declined from the early years of the study to the later years (Figure 2): the mean probability of capture in the various passes during 1991–2000 (mean = 0.094; n = 21) significantly differed (P < 0.0001) from the mean probability of capture during passes of 2003–2010 (mean = 0.055; n = 27). Mean annual capture probability (probability that an individual fish would be captured in a given year) for the entire study period was higher in the upper reach (mean = 0.241) than in the lower reach (mean = 0.191; Appendix Table II).

Survival Rate

The top model for the 2004–2010 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. Because of this, annual survival estimates were the same for all time intervals: 2005–2008, 2008–2009, and 2009–2010. 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). These earlier estimates were for Colorado pikeminnow ≥ 500 mm TL (the top model included a length effect). The most recent estimate, for 2008–2010, was 88.4% and included all fish in the capture-history matrix (≥ 250 mm TL) because a length effect was not supported by the top model (however, for the upper reach, all but two fish were ≥ 500 mm TL). For the upper reach, there were no significant differences in annual survival rate estimates among the four

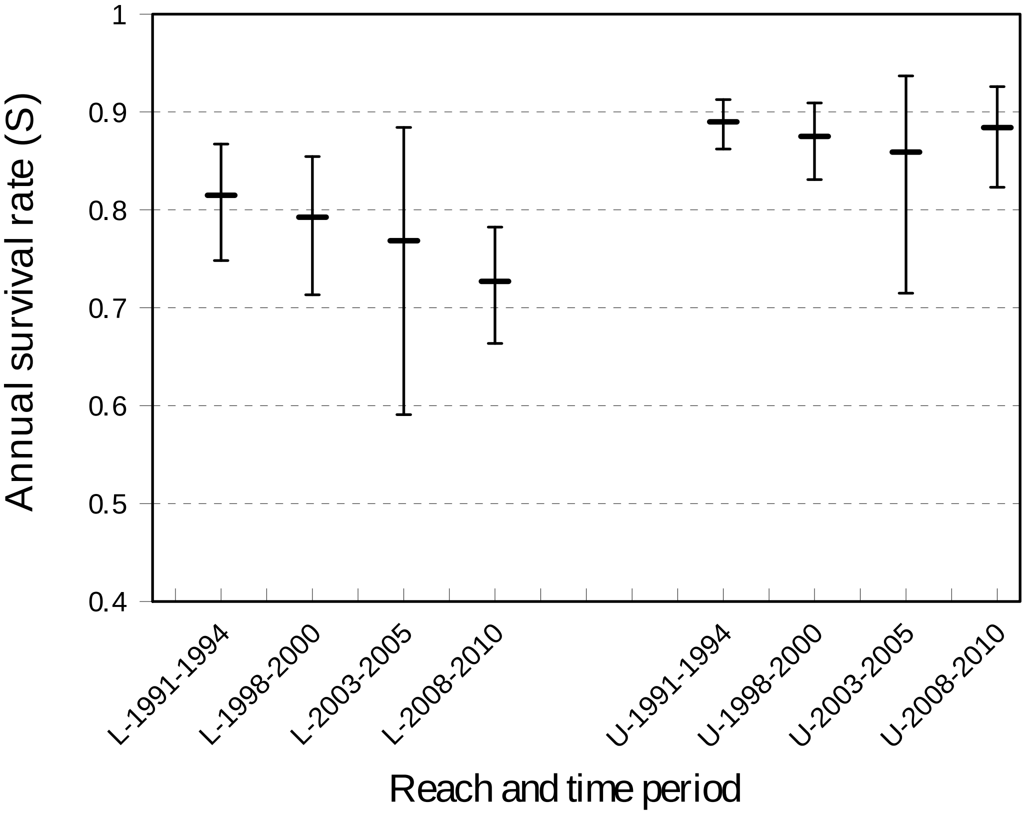

Figure 3. Annual survival rate (*S*) estimates of Colorado pikeminnow ≥ 500 mm TL by reach (upper: U; lower: L) for the three earlier multi-year periods, and for Colorado pikeminnow ≥ 250 mm TL for the recent 2008–2010 period. Error bars represent the 95% confidence interval.

multi-year periods. In the lower reach, annual survival rate point estimates declined by eight percentage points through the four multi-year sampling periods (1991–1994: 81.5%; 1998–2000: 79.3%; 2003–2005: 76.9%; 2008–2010: 72.7%), but estimate differences were not statistically significant. The earlier three estimates were for fish ≥ 500 mm TL; the fourth estimate was for fish ≥ 250 mm TL.

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 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 point estimates for the lower reach ranged from 299 (2010) to 1,192 (2003), and for the upper reach, from 217 (1991) to 484 (2005); summed estimates ranged from 585 (2009) to 1,516 (2003). For individuals ≥ 450 mm TL, abundance estimates ranged from 160 (1992) to 492 (1993) in the lower reach and 202 (1991) to 477 (2005) in the upper reach; summed estimates ranged from 440 (1992) to 889 (2005). For fish ≥ 500 mm TL, estimates ranged from 75 (1992) to 297 (2003) in the lower reach and from 175 (1993) to 407 (2008) in the upper reach; summed estimates ranged from 334 (1992) to 661 (2008).

Based on non-overlap of 95% confidence intervals, only a few abundance estimates were significantly different from one another (Figure 4). In the lower reach, the abundance estimate for Colorado pikeminnow ≥ 250 mm TL was significantly higher in 2003, the year in which they appeared to reach their greatest abundance, than in all three recent study years, 2008-2010 (not shown, but see Appendix Table III). Within the upper reach, 1998, 1999, and 2005 abundance estimates were significantly higher than the 1993 estimate for Colorado pikeminnow ≥ 250 mm TL (Appendix Table III) and for those ≥ 450 mm TL (Figure 5). Also in the upper reach, the 2009 abundance estimate for individuals ≥ 450 mm TL was significantly lower than the estimate for 2005. For the two reaches combined, point estimates for Colorado pikeminnow ≥ 250 mm TL were significantly lower in all three recent years than in 2003 (Appendix Table III). For those ≥ 450 mm TL, combined abundance estimates were significantly lower in the two most recent study years (2009 and 2010) than in 2005, the year this size group appeared to be most abundant (Figure 4). For Colorado pikeminnow ≥ 500 mm TL, there were no significant differences among combined estimates (Figure 4).

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. For all three major length groups described above, nine of 12 annual CVs for the summed-reach estimates were < 20%. For Colorado pikeminnow ≥ 450 mm TL, the overall mean CV of the twelve annual combined-reach estimates was 16.8%. During the most recent three-year effort (2008–2010), the mean CV

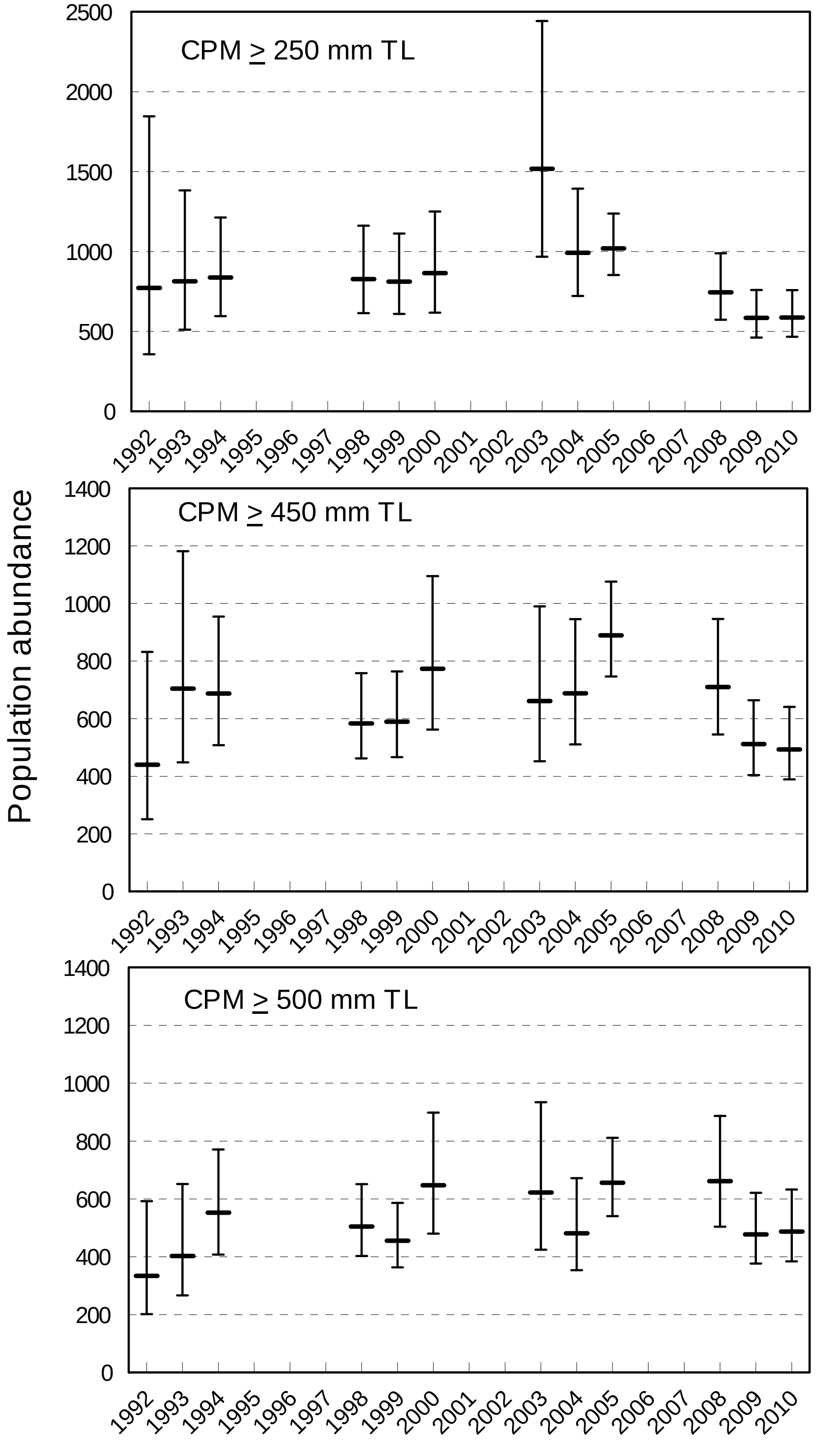

Figure 4. Abundance estimates of Colorado pikeminnow of three length classes: ≥ 250 mm TL; ≥ 450 mm TL; ≥ 500 mm TL in the upper Colorado River study area (reaches combined), 1992–2010. Annual population abundance estimates shown were derived by summing separate estimates for the lower and upper reaches (see Appendix Tables III, IV and V for numbers). Error bars represent the 95% confidence interval.

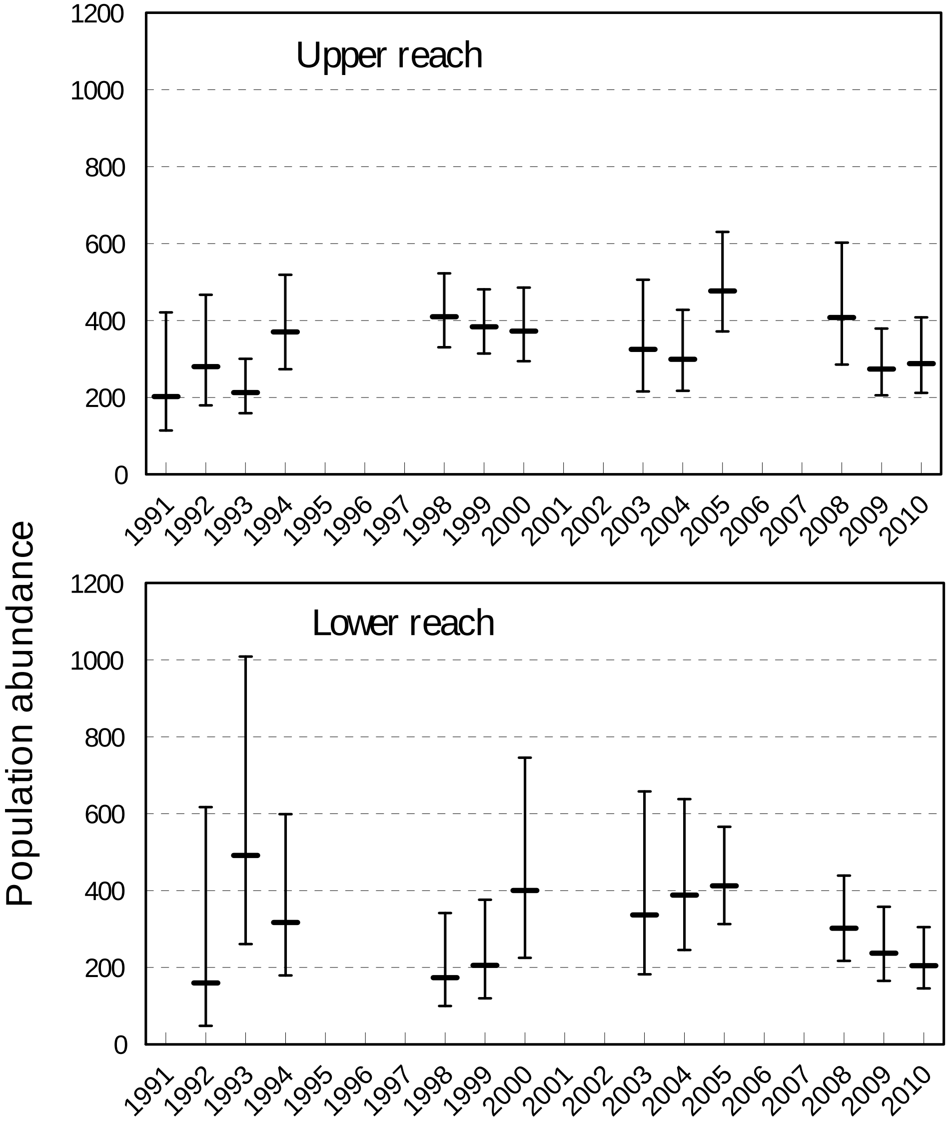

Figure 5. Abundance estimates of Colorado pikeminnow ≥ 450 mm TL in the upper (top panel) and lower (bottom panel) Colorado River study reaches, 1991–2010 (see Appendix Tables IV for numbers). Error bars represent the 95% confidence intervals.

for this length group was 13.2%, the best (lowest) of any of the four multi-year efforts (first three years: 25%; second three years, 14.3%; third three years, 15.2%). However, the best single year for this length group was 2005, with a CV of 9.4%.

From an earlier analysis by Osmundson and White (2009), a variance components trend analysis indicated fish ≥ 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 2008–2010 indicated Colorado pikeminnow 400–449 mm TL (Recovery Goals criterion for fish about to recruit) were not present in the upper reach during these years (Figure 6). In the lower reach, the three recent annual estimates ranged from seven to 19 individuals. Because this length group is a fairly small subset of the total population, captures and recaptures were very limited, resulting in wide confidence intervals around $\hat{N}$, 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 (if only in a general way) 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%. For years 2008–2010, we applied the lower-reach mortality rate (27.3%) to the lower reach abundance estimate and the upper-reach mortality rate (11.6%) to the upper-reach abundance estimate. Results indicated an estimated loss of 82 fish $\geq$ 450 mm TL from apparent mortality in the lower reach during 2008 and a gain of 19 fish from recruitment, for a net loss of 63 fish. In the upper reach, there was an estimated loss of 47 fish and no recruitment in 2008. In 2009, there was an estimated net loss of 57 fish $\geq$ 450 mm TL in the lower reach (mortality loss of 65; recruitment gain of 8) and a net loss of 32 fish in the upper reach (all

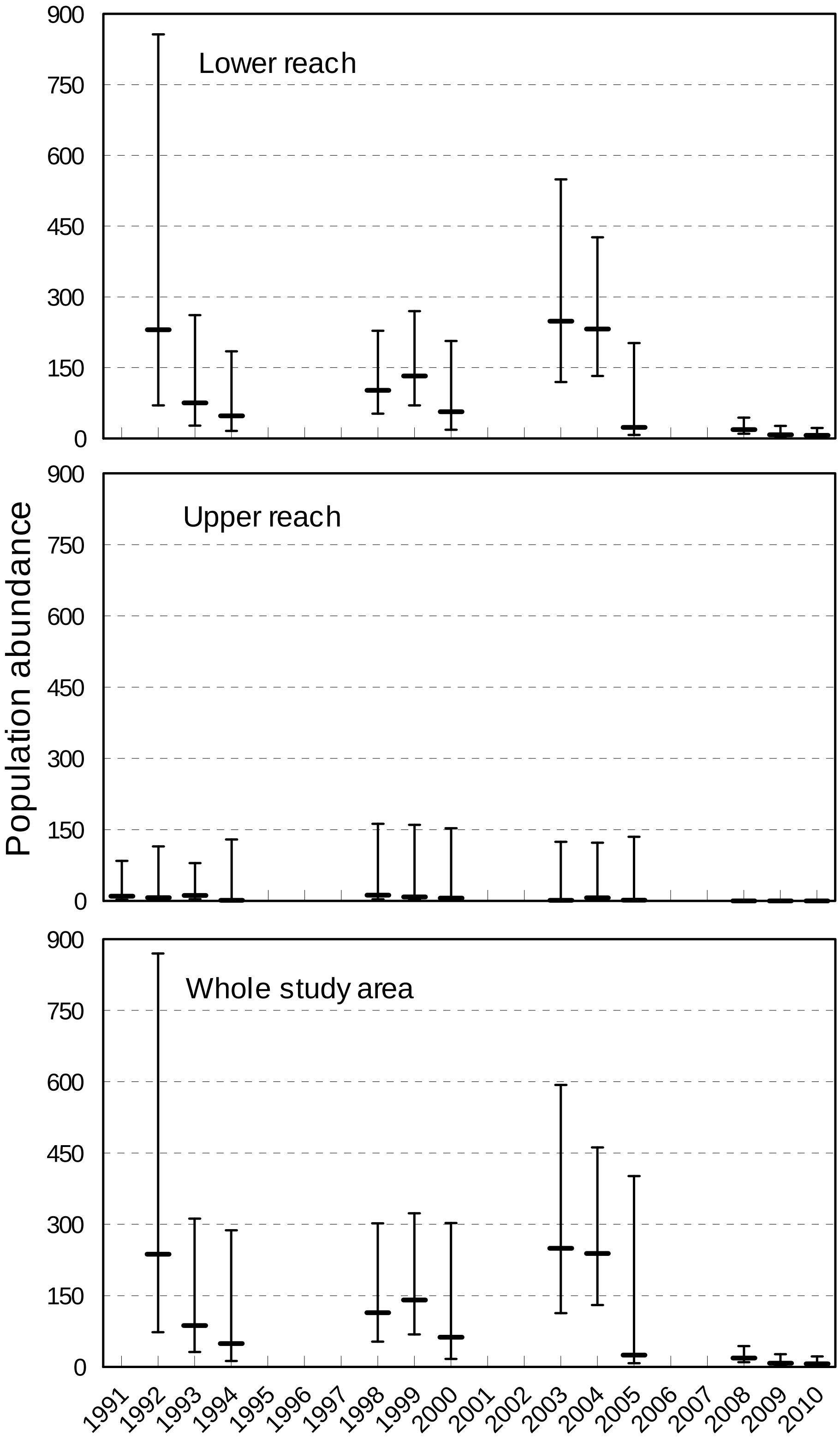

Figure 6. Annual abundance estimates of Colorado pikeminnow 400–449 mm TL in the lower, upper, and combined reaches, 1991–2010 (see Appendix Tables VI for numbers).

mortality; no recruitment). In 2010, there was an estimated net loss of 49 fish $\geq$ 450 mm TL (56 fish loss from mortality; 7 fish gain from recruitment) in the lower reach and an estimated net loss of 33 fish in the upper reach (all from mortality). Hence, for the study area as a whole, there were estimated net losses of 129 fish in 2008, 89 fish in 2009, and 82 fish in 2010. Of the 12 years studied, there were estimated gains in six of the years, and losses in the other six years (Figure 7). Gains ranged from 1 to 183 individuals per year; losses, from 35 to 129 individuals per year. The estimated net gain for the 12 years studied was 32 fish $\geq$ 450 mm TL. Because estimates were not available for 1995–1997, 2001–2002, and 2006–2007, total gain or loss for the 19-year period could not be estimated. Although seven years were missing and estimates we have are approximations, the net gain reported is generally supported by the combined-reach population estimates for fish $\geq$ 450 mm TL: $\hat{N} = 440$ in 1992 and $\hat{N} = 493$ in 2010 (estimated gain of 53 fish).

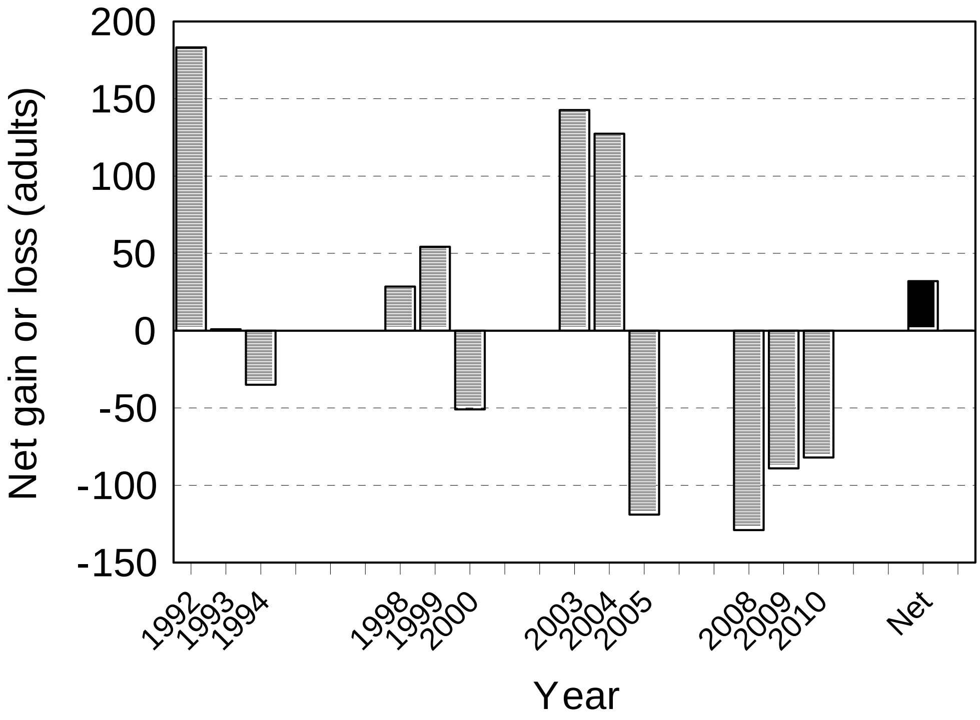

Figure 7. Estimated annual net gain or loss of Colorado pikeminnow $\geq$ 450 mm TL in the Colorado River population (upper and lower reaches combined). Values are based on the estimated number of fish 400–499 mm TL present each year minus the estimated number of deaths of fish $\geq$ 450 mm TL.

Population trend analysis of the lower-reach sub-population of Colorado pikeminnow ≥ 450 mm TL using weighted regression of abundance estimates over the four multi-year study periods indicated most support (weight = 0.83) for the intercept-only model, limited support (weight = 0.14) for the linear model, and very little support (weight = 0.03) for the quadratic model (Table 4; Figure 8). These results suggest the lower-reach subpopulation was relatively stable over the 19-year period. In the upper reach, however, weighted regression indicated strongest support for the quadratic model (weight = 0.65), less support for the intercept-only model (weight = 0.27) and little support for the linear model (weight = 0.08). Model coefficients suggest a significant increase (large and positive quadratic coefficient relative to the standard error) in the upper reach sub-population followed by a significant decline (large and negative quadratic coefficient relative to the standard error) over the 20-year period. For the Colorado River population as a whole (lower and upper sub-populations of Colorado pikeminnow ≥ 450 mm TL combined), weighted regression of summed abundance estimates indicated strongest support for the intercept-only model

Table 4. Intercept only (*I*), linear (*I, T*), and quadratic (*I, T, T^2*) regression relationship estimates of abundance estimates for years 1991–1994, 1998–2000, 2003–2005 and 2008–2010 for Colorado pikeminnow ≥ 450 mm TL.

Reach	Model	df	Intercept (SE)	Time (SE)	Time2 (SE)	Weight
Lower	*I*	1, 11	252.5 (30.5)			0.83
	I, T	2, 11	229.9 (88.4)	1.5 (5.5)		0.14
	I, T, T^2	3, 11	77.8 (155.6)	33.7 (27.9)	-1.3 (1.1)	0.03
Upper	*I*	1, 12	311.8 (26.1)			0.27
	I, T	2, 12	276.5 (47.1)	3.6 (4.0)		0.08
	I, T, T^2	3, 12	153.4 (55.6)	39.9 (12.9)	-1.7 (0.6)	0.65
Combined	*I*	1, 11	608.1 (45.9)			0.78
	I, T	2, 11	637.7 (116.0)	-2.2 (7.8)		0.13
	I, T, T^2	3, 11	362.0 (186.2)	58.6 (34.8)	-2.5 (1.4)	0.09

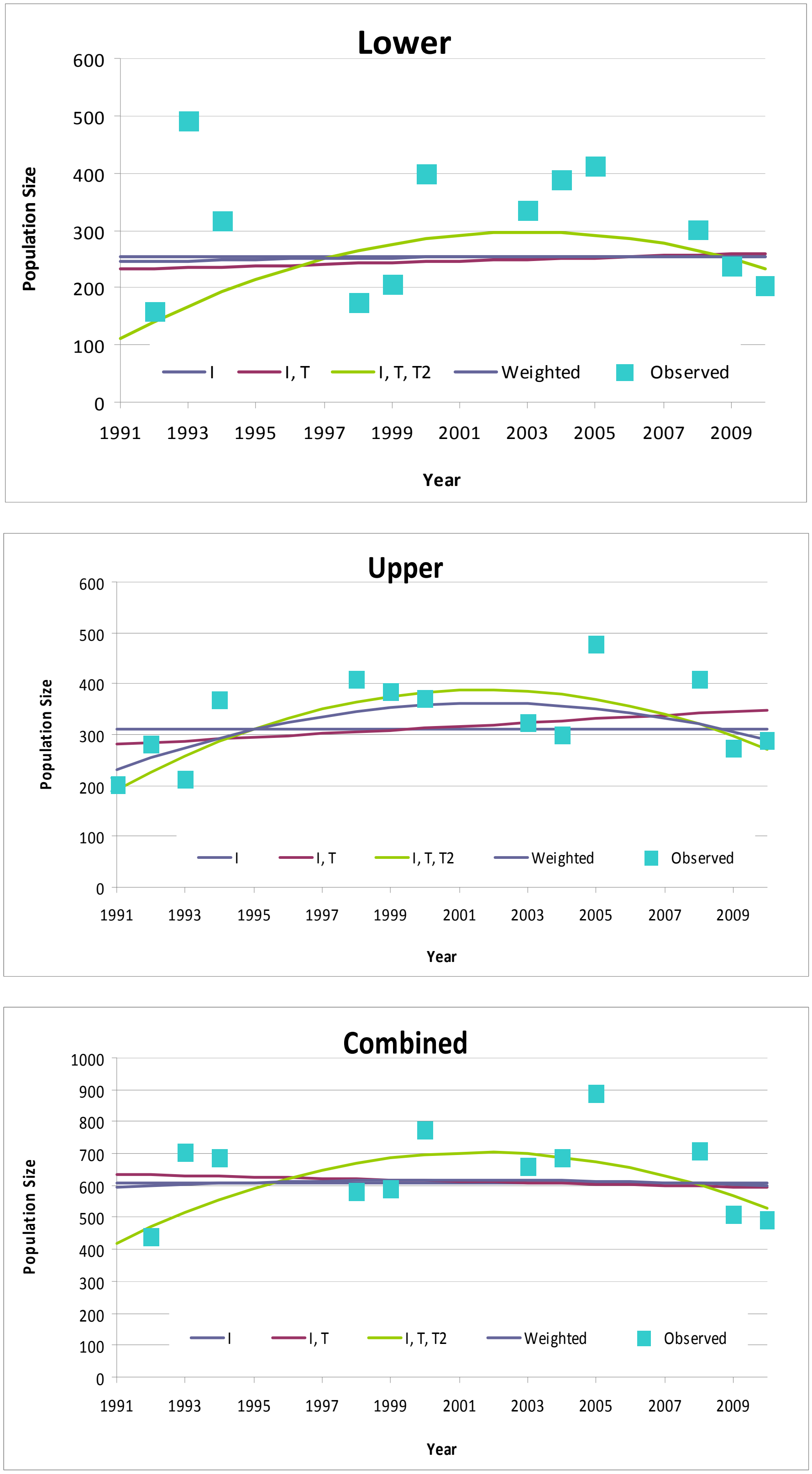

Figure 8. Abundance trends of Colorado pikeminnow ≥ 450 mm TL in the lower (top), upper (middle), and combined (bottom) Colorado River study reaches, 1991–2010.

(weight = 0.78), and limited support for the linear (weight = 0.13) and quadratic (weight = 0.09) models. In all three cases (lower-reach, upper-reach and combined reach populations), the linear models had standard errors larger than the corresponding coefficients indicating possible long-term increases or decreases were non-significant.

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 48 such movements and seven 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.

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. Then, from 2004 to 2005, the probability of a lower-reach, 500-mm-long fish moving to the upper reach jumped to 30%.

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%. Again, much of this movement may have occurred early in the interval because during the two subsequent annual intervals

Table 5. Annual (1991–2009) 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	Movement		
		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	0.0227[3]	0.0000	0.0227
2006	2007	0.0227[3]	0.0000	0.0227
2007	2008	0.0227[3]	0.0000	0.0227
2008	2009	0.1974[4]	-----[5]	----[5]
2009	2010	0.1974[4]	-----[5]	----[5]

[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] Average per year calculated from single value for period 2005–2008 because of un-sampled years

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

[5] Values are unrealistically high due to extremely sparse data and are considered unreliable.

(2003 to 2004 and 2004 to 2005) probabilities of movement to the lower reach were again 0%.

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 (Table 6), suggesting that few smaller individuals made the lower-to-upper reach transition.

Table 6. Total lengths of Colorado pikeminnow before and after movement from the lower reach to the upper reach of the Colorado River study area. Only those fish moving between reaches based on capture-recapture in consecutive years are included; RM = river miles from the confluence; GU = Gunnison River.

	Lower reach capture			Upper reach capture		
Fish ID number	Year	Location (rm)	Length (mm)	Year	Location (RM)	Length (mm)
129	1992	81.5	438	1993	175.2	478
186	1992	98.9	421	1993	154.3	449
238	1993	58.2	523	1994	147.1	540
323	1993	26.5	456	1994	GU-1.1	466
837	2003	43.1	402	2004	135.5	445
851	2004	49.9	411	2005	150.7	459
990	2004	72.7	435	2005	159.6	487
991	2004	66.4	472	2005	183.0	495
993	2004	67.4	451	2005	169.8	474
1004	2004	39.6	477	2005	162.8	511
503	2008	99.8	573	2009	135.1	581
520	2008	38.5	715	2009	GU-2.3	726
529	2008	64.7	485	2009	167.6	509
286	2009	45.0	600	2010	185.5	617

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 improve AICc of the top model and thus was not used for estimating abundance or survival.

Because the new 2004–2010 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. As before, only one transition probability (6.8%) could be estimated for the non-sampled period between 2005 and 2008, so these movements were distributed equally over the three years providing annual estimates of 2.3%. The new matrix did not indicate a time effect so probabilities for lower-to-upper transitions for periods 2008–2009 and 2009–2010 were identical (19.7%). For upper-to-lower reach transitions, the data were so sparse in the new reduced matrix that the probabilities calculated were considered unreliable and were not reported (Table 5).

Electrofishing Catch-per-Effort

Mean electrofishing catch rates (Colorado pikeminnow $\geq$ 250 mm TL/hr of electrofishing) per pass were fairly consistent across the three recent study years (Figure 9). Variance about each mean was generally higher in the upper reach than in the lower reach. Within reaches, mean catch rates did not differ significantly among passes. In the lower reach, most passes had a mean catch rate of 0.25 fish/hr or less; in the upper reach, most passes had a mean catch rate higher than 0.25 fish/hr. All passes in both reaches had mean catch rates < 0.5 fish/hr. There was no consistent trend of catch rates either increasing or decreasing within years as spring sampling progressed.

Mean annual catch rates increased from 2003 to 2005 in the upper and lower reaches and in the two reaches combined, but then declined (Figure 10). In the upper reach, mean

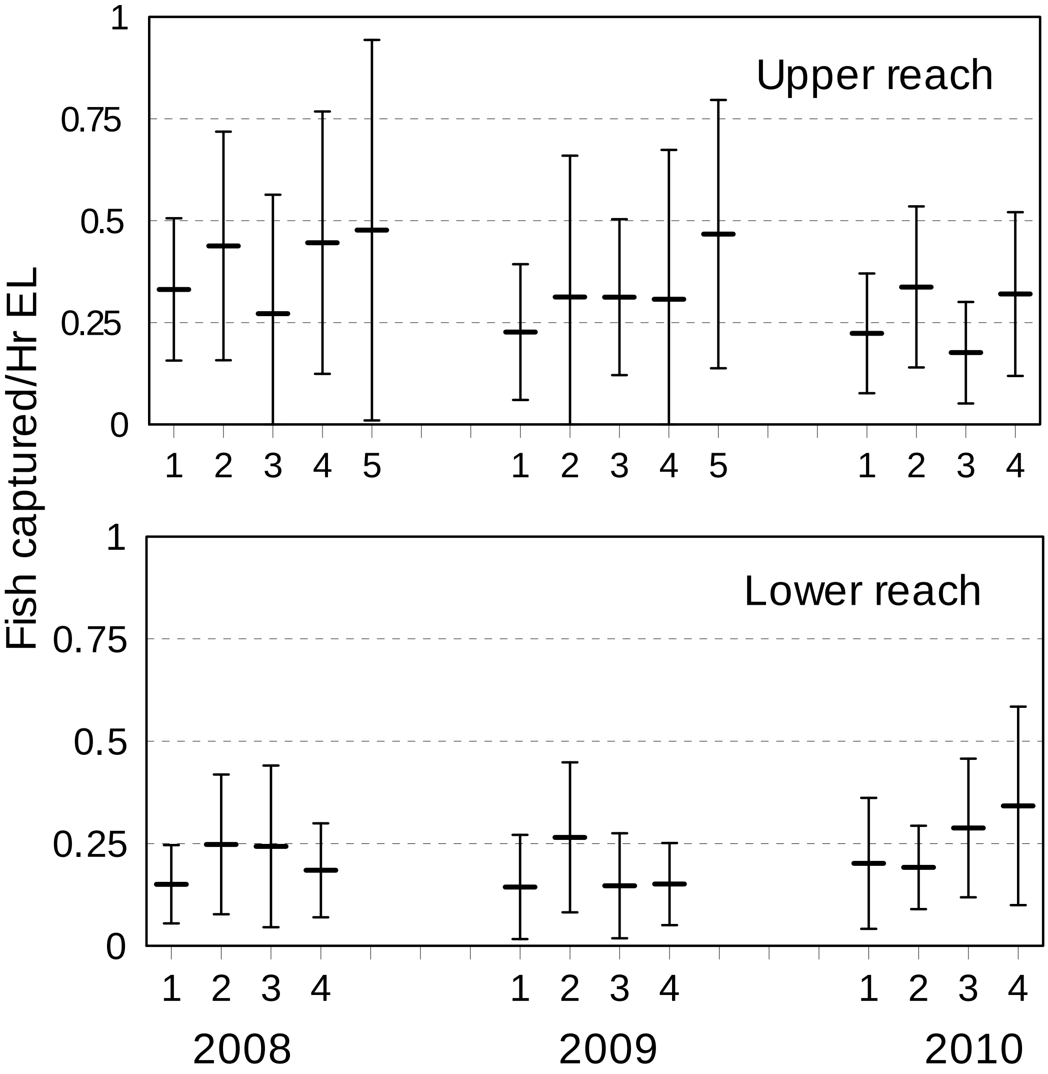

Figure 9. Electrofishing mean catch rates (fish/hr) of Colorado pikeminnow (≥ 250 mm TL) per sampling pass in the upper (top) and lower (bottom) reaches of the Colorado River study area, 2008–2010. Samples within each pass consisted of one electrofishing boat day (typically, an individual crew working one shoreline within a standardized daily sampling river segment; in some passes, some segments were sampled more than once). Error bars represent the 95% confidence interval about the mean.

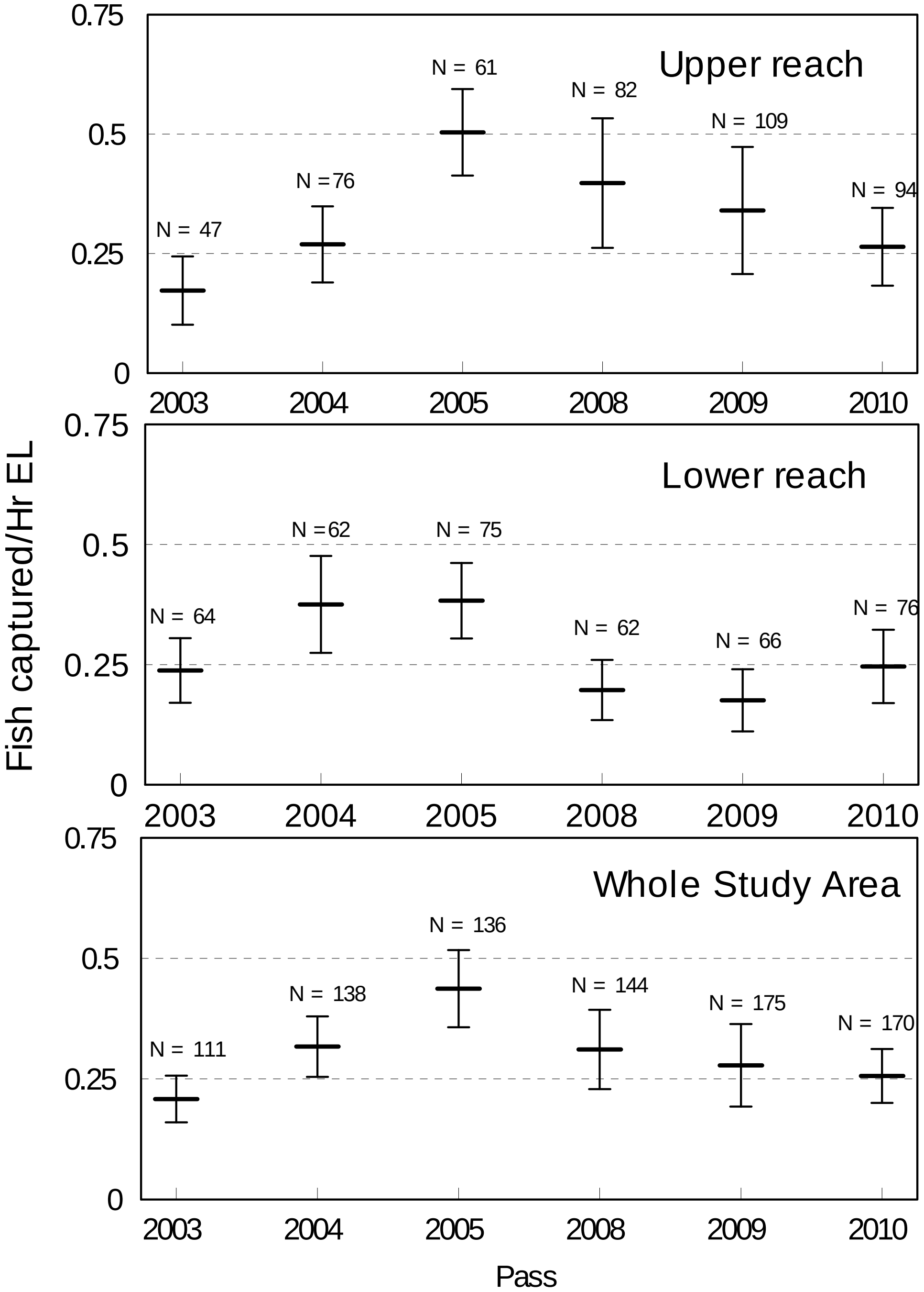

Figure 10. Electrofishing mean catch rates (fish/hr) of Colorado pikeminnow (≥ 250 mm TL) in the upper (top), lower (middle), and combined (bottom) reaches of the Colorado River study area, 2003–2005 and 2008–2010. Daily catch rates were pooled by year. Sample sizes (N) are boat days of electrofishing (i.e., typically, an individual crew working one shoreline within a standardized daily sampling river segment). Means are arithmetic means. Error bars represent the 95% confidence interval about the mean.

annual catch rate was significantly higher in 2005 than it was in 2003 and 2004; in the lower reach, mean annual catch rate in 2005 was significantly higher than in 2003. When all daily catch rates were pooled by year (upper and lower reaches combined), the mean catch rates for 2004 (0.32 fish/hr) and 2005 (0.43 fish/hr) were significantly higher than in 2003 (0.21 fish/hr). This trend was reversed during the 2008–2010 period. In the upper reach, mean annual catch rate in 2010 was significantly lower than in 2005. In the lower reach, mean annual catch rates in 2008 and 2009 were significantly lower than in 2005. Similarly, when all daily catch rates were pooled by year (reaches combined), the mean annual catch rate for the whole study area in 2010 (0.26 fish/hr) was significantly lower than in 2005 (0.43 fish/hr).

As expected, river-wide, electrofishing catch rates for all Colorado pikeminnow ≥ 250 mm TL were higher (but not significantly so) than for those ≥ 450 mm TL (Figure 11). However, in years 2008 and 2009, differences were very little, indicating that captures of fish 250–449 mm TL made up a relatively small proportion of the overall catch.

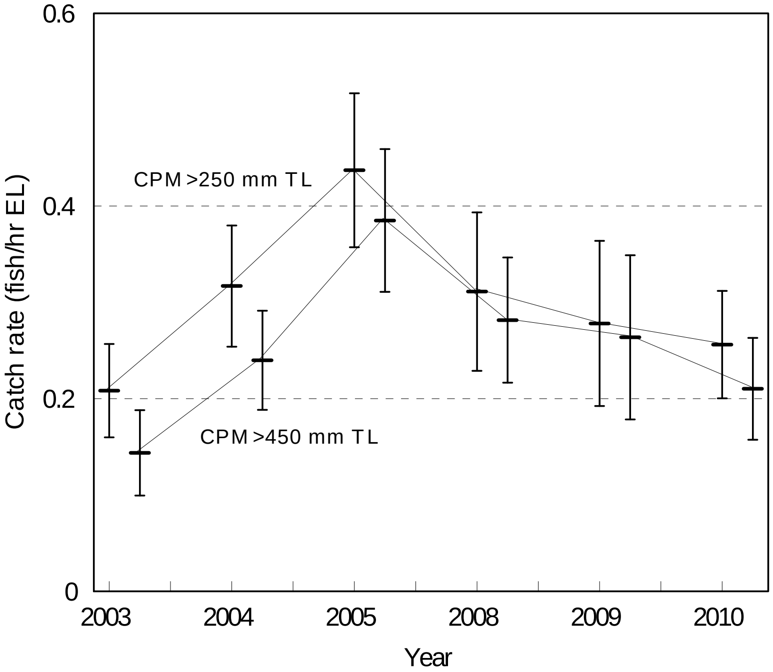

Figure 11. Electrofishing mean catch rates (fish/hr) of Colorado pikeminnow ≥ 250 mm TL and of those ≥ 450 mm TL. Data from the upper and lower reaches were combined to come up with mean annual rates for the entire Colorado River study area.

When the trend of mean annual catch rates was compared to the annual abundance point estimates, there was good agreement for years 2005 and later, but poor agreement for 2003 (Figure 12). How well these indices tracked one another varied by the length group included in the comparison. For fish ≥ 250 mm TL, population point estimates indicated comparatively high abundance in 2003 and 2004, but this was not indicated by catch rate results. For all three size groups, catch rates increased after 2003, reached a peak in 2005, and then declined. The best overall fit between catch rates and abundance estimates appeared to be for fish ≥ 450 mm TL. The smallest decline in catch rates from the 2005 peak was for Colorado pikeminnow ≥ 500 mm TL.

Trammel-Net Catch-Per-Effort

The number of trammel nets set varied by reach and year. In both reaches, no netting was done in 2004. In other years, number of nets per year ranged from 38 (1991) to 291 (2009) in the lower reach; 51 (2005) to 145 (1998) in the upper reach. In the lower reach, Sagar's Wash (RM 99.0), Kane Springs Creek (RM 58.0), and Indian Creek (RM 16.5) were especially productive sites for capturing Colorado pikeminnow. In the upper reach, many adults were captured during the early monitoring years from the ponds at Walker State Wildlife Area (WSWA; RM 163.5–164.7) and Island Backwater (RM 175.5–176.0). At the WSWA ponds, there was a total of 106 trammel-net captures of Colorado pikeminnow during the first two sampling periods. At Island Backwater, there was a total of 57 captures. Together, this comprised 27% of all upper-reach trammel-net captures from 1991 through 2000 (Table 7).

Trends in netting catch-per-unit-effort of Colorado pikeminnow (mean number of fish caught per net set) appeared to differ between lower and upper reaches (Figure 13). In the lower reach, where there was often a high number of individuals < 450 mm TL, catch rates in 1999 were significantly lower than in 1998, and catch rates in 2008 and 2009 were significantly lower than in four previous years (1993, 1994, 1998 and 2000). Although most years were not significantly different from one another, there was an overall downward trend in netting catch rates during the 19-year period (11 net-sampling years).

In the upper reach, where individuals were almost exclusively ≥ 450 mm TL, catch rates increased from 1991 through 2000, but then dropped off sharply. The catch rate in

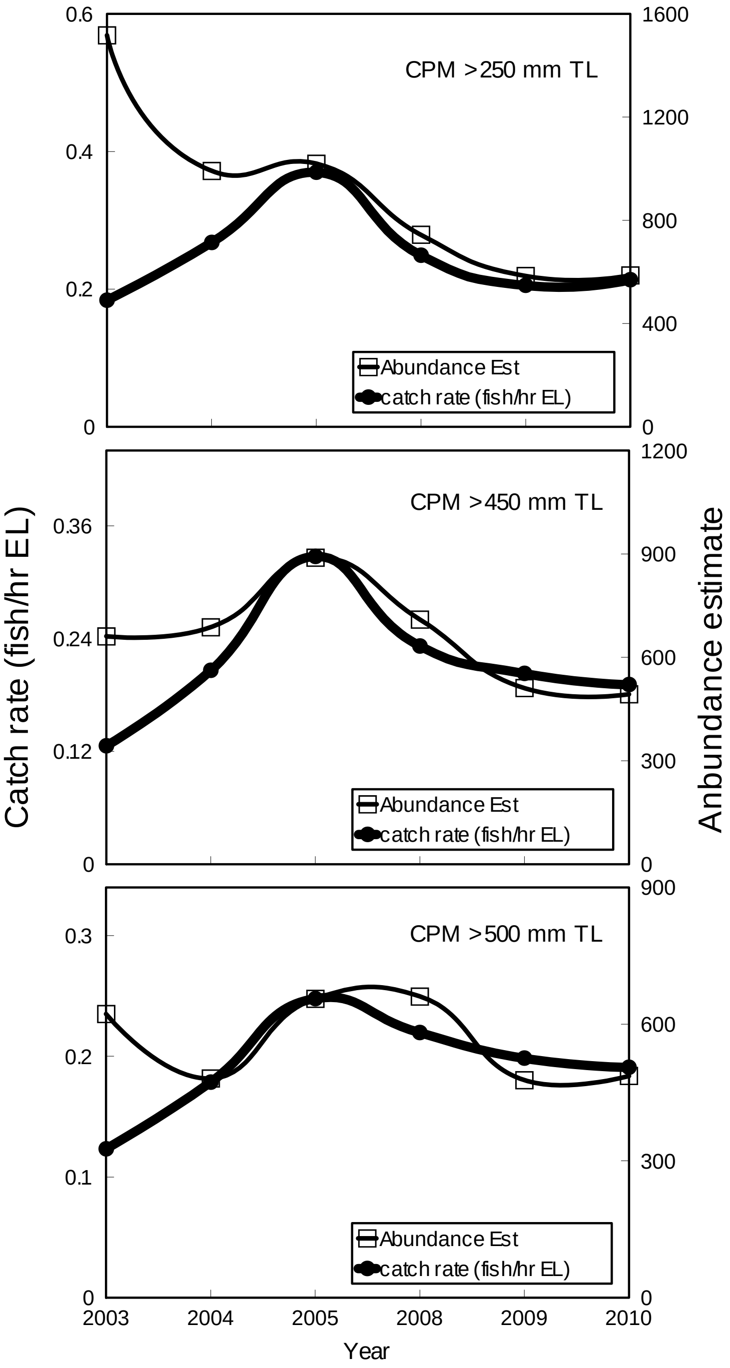

Figure 12. Annual mean electrofishing catch rates of Colorado pikeminnow (upper and lower study reaches combined) compared with annual mark-recapture-based abundance point estimates for years 2003–2005 and 2008–2010. Catch rates are geometric means because daily catch rates were non-normally distributed (high proportion of daily catch rates equal to zero); daily catch rates were first log-transformed using *ln*(fish/hr EL + 1), the anti-log of the mean taken, and one subtracted from the result. The mean catch rate and abundance estimate of 2005 were arbitrarily superimposed on the graph for use as a reference point for viewing the two trend lines in relation to each other.

Table 7. Captures of Colorado pikeminnow at two sites in the upper-reach study area and the percent contribution of these captures to the total upper-reach trammel-net captures, 1991–2000.

Year	Total trammel captures	Walker site captures	Percent captures from Walker	Island BA site captures	Percent captures from Island BA	Percent captures from both sites
1991	48	1	2.1	2	4.2	6.3
1992	57	9	15.8	6	10.5	26.3
1993	75	34	45.3	3	4.0	49.3
1994	70	18	25.7	7	10.0	35.7
1998	142	32	22.5	16	11.3	33.8
1999	107	5	4.7	10	9.3	14.0
2000	87	7	8.0	13	14.9	22.9
mean	83.7	15.1	17.7	8.1	9.2	26.9

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. Mean catch rates during 2008-2010 were significantly lower than those during 1998-2000. In fact, the mean catch rate in 2010 was significantly lower than in all years during the 1990's.

Trends in netting catch rates did not support trends in abundance point estimates in either reach. In the lower reach, mean catch rates were highest in 1992 and 1998, yet 1993 had the highest abundance estimate. There was a clear decline in netting catch rates (r^2 = 75; P = 0.0006) when mean number of captures per net was regressed against year, yet no such decline (r^2 = 0.03; P = 0.60) was evident when abundance estimates were similarly regressed against year (Figure 14).

In the upper reach, mean netting catch rate of Colorado pikeminnow was highest in 1998, yet mark-recapture abundance estimates indicated highest abundance in 2005. A significant upward trend (r^2 = 0.90; P = 0.01) in catch rates from 1991 through 1998

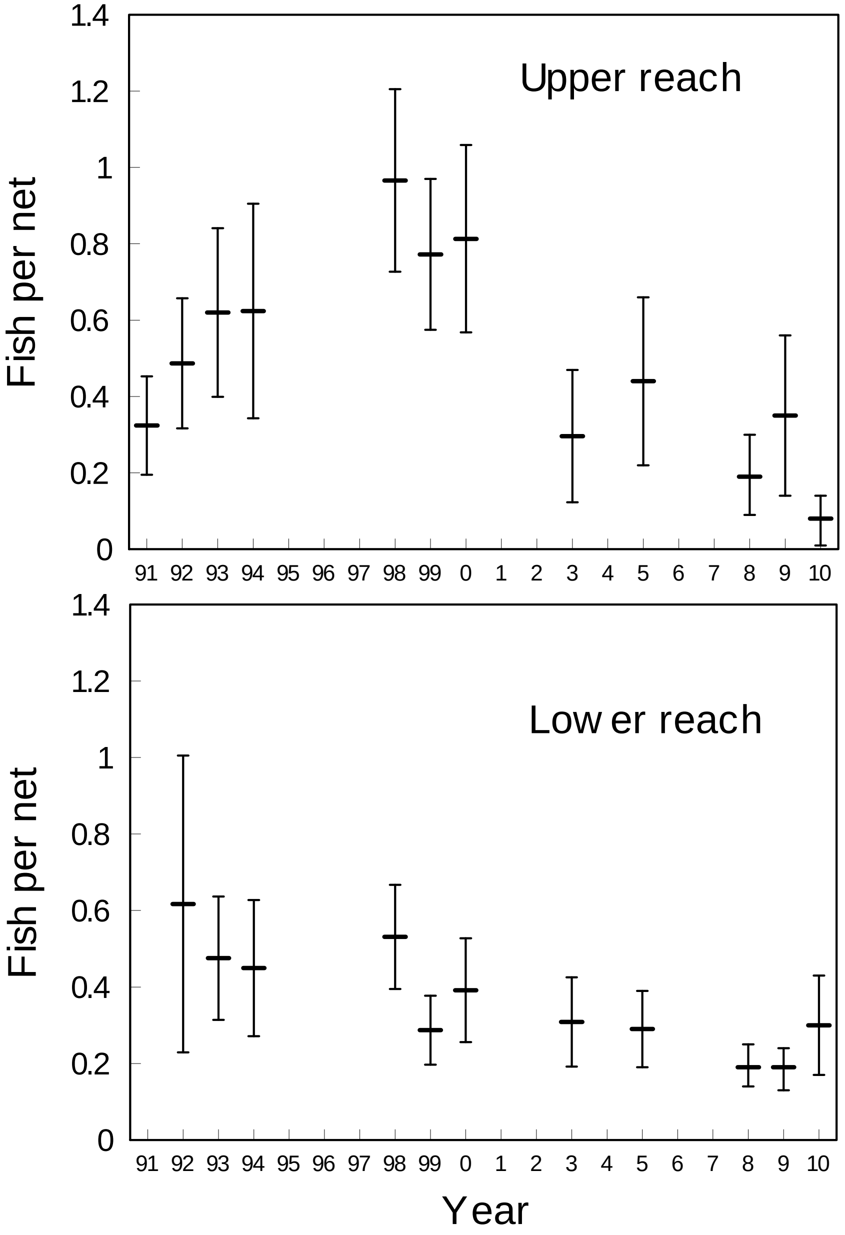

Figure 13. Trammel net catch rates (mean number of fish per net set) of Colorado pikeminnow in the lower- and upper-reach Colorado River study areas, 1991–2010.

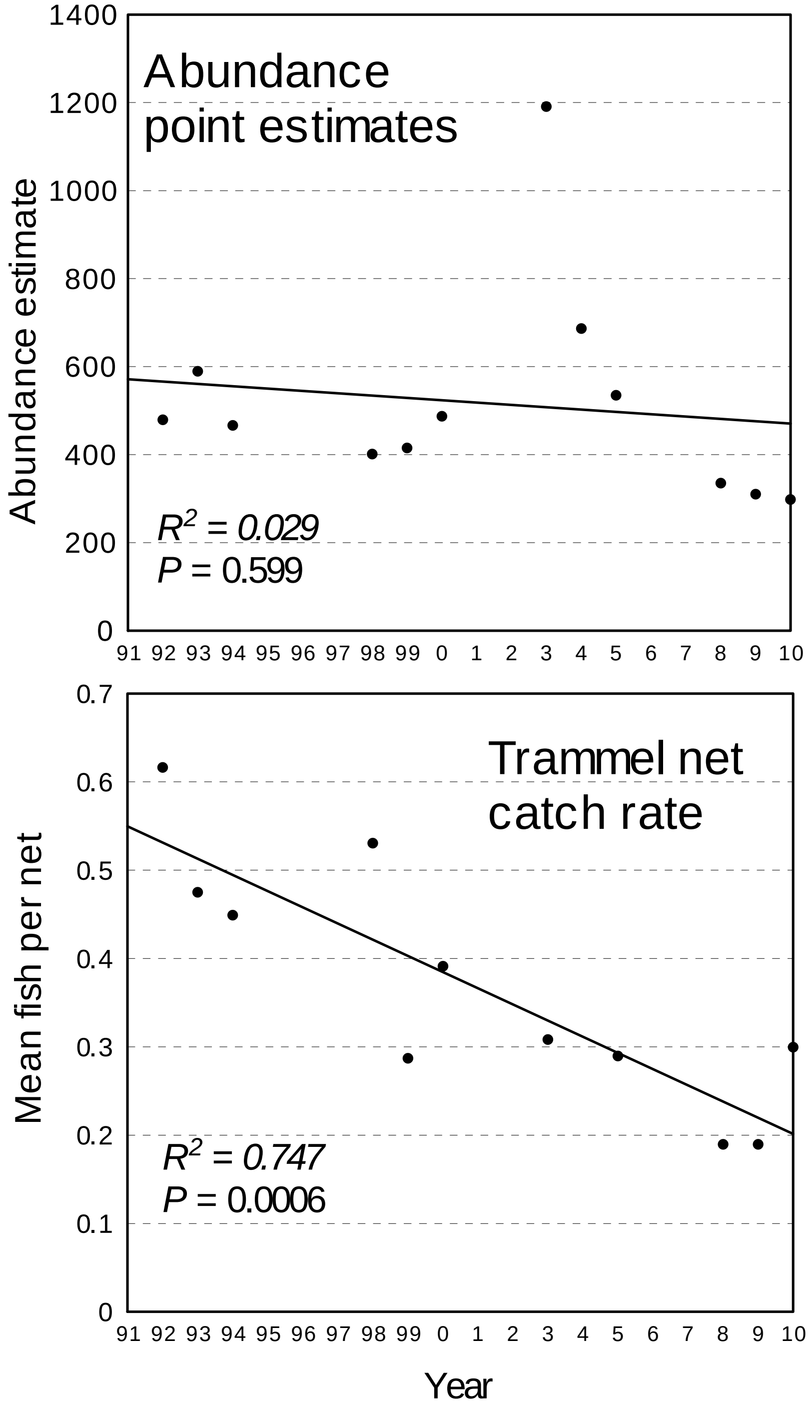

Figure 14. Trends in trammel net catch rates (fish/net set) and population estimates for the lower reach of the Colorado River study area, 1992–2010.

was followed by a significant downward trend from 1998 through 2010 ($r^2 = 0.82$; $P = 0.002$). Abundance estimates also displayed an increasing trend followed by a decreasing trend, but the year when trend lines changed direction differed between the two indices. A weak but significant upward trend ($r^2 = 0.41$; $P = 0.046$) in abundance point estimates from 1991 through 2005 was followed by a strong, though not quite significant ($r^2 = 0.86$; $P = 0.072$), downward trend from 2005 through 2010 (not shown). In summary, upper-reach netting catch rates declined after 1998, while abundance estimates declined after 2005.

Catch rates of Sympatric Species

Trammel-netting catch rates of species that share backwater habitat with Colorado pikeminnow suggest some changes in density during the overall 19-year study period. Species common to zero-velocity habitats (downstream pooled end of dewatered side channels, flooded canyon mouths, and riverside gravel-pit ponds) include natives: flannelmouth sucker (*Catostomus latipinnis*), bluehead sucker (*Catostomus discobolus*), and roundtail chub (*Gila robusta*); and non-natives: common carp (*Cyprinus carpio*), channel catfish (*Ictalurus punctatus*), white sucker (*Catostomus commersonii*), and black bullhead (*Ictalurus melas*). Sympatric species were generally sparse in lower-reach net catches. The most common species found in trammel nets in the upper reach was flannelmouth sucker followed by common carp and roundtail chub (Figure 15). Mean annual capture rates of flannelmouth sucker ranged from 2.0 to 6.4 fish/net, depending on the year; roundtail chub, from 0.8 to 3.2 fish/net; bluehead sucker, from 0.2 to 0.9 fish/net (Figure 16). Common carp annual catch rates ranged from 1.7 to 4.4 fish/net; black bullhead, from 0.6 to 2.5 fish/net; white sucker, from 0.3 to 1.8 fish/net; channel catfish, from 0.2 to 0.7 fish/net (Figure 17).

Three of the seven most common species captured in trammel nets displayed a significant downward trend in catch rate during the 19-year period (Figure 18). These were roundtail chub ($r^2 = 0.74$; $P = 0.0007$), common carp ($r^2 = 0.53$; $P = 0.01$), and channel catfish ($r^2 = 0.38$; $P = 0.04$). Trends in catch rates of flannelmouth sucker ($r^2 = 0.05$; $P = 0.47$), bluehead sucker ($r^2 = 0.14$; $P = 0.27$), white sucker ($r^2 = 0.17$; $P = 0.21$), and black bullhead ($r^2 = 0.18$; $P = 0.19$) were relatively flat (not shown).

Other non-native species, though less abundant, may be (or may become) ecologically important components of the Colorado River fish assemblage. These include smallmouth bass *Micropterus dolomieu*, largemouth bass *Micropterus salmoides*, walleye *Stizostedion vitreum*, northern pike *Esox lucius*, gizzard shad *Dorosoma cepedianum*, grass carp *Ctenopharyngodon idella*, black crappie *Pomoxis nigromaculatus*, bluegill *Lepomis macrochirus* and green sunfish *Lepomis cyanellus*. Gizzard shad is a recent invader of the study area and by 2010 was commonly caught in the lower reach by both electrofishing and trammel netting (Figure 19). Predacious centrarchids were caught in small numbers in the lower reach, but had become common and widespread throughout the upper reach: 363 smallmouth bass and 100 largemouth bass were captured and removed during 2008-2010.

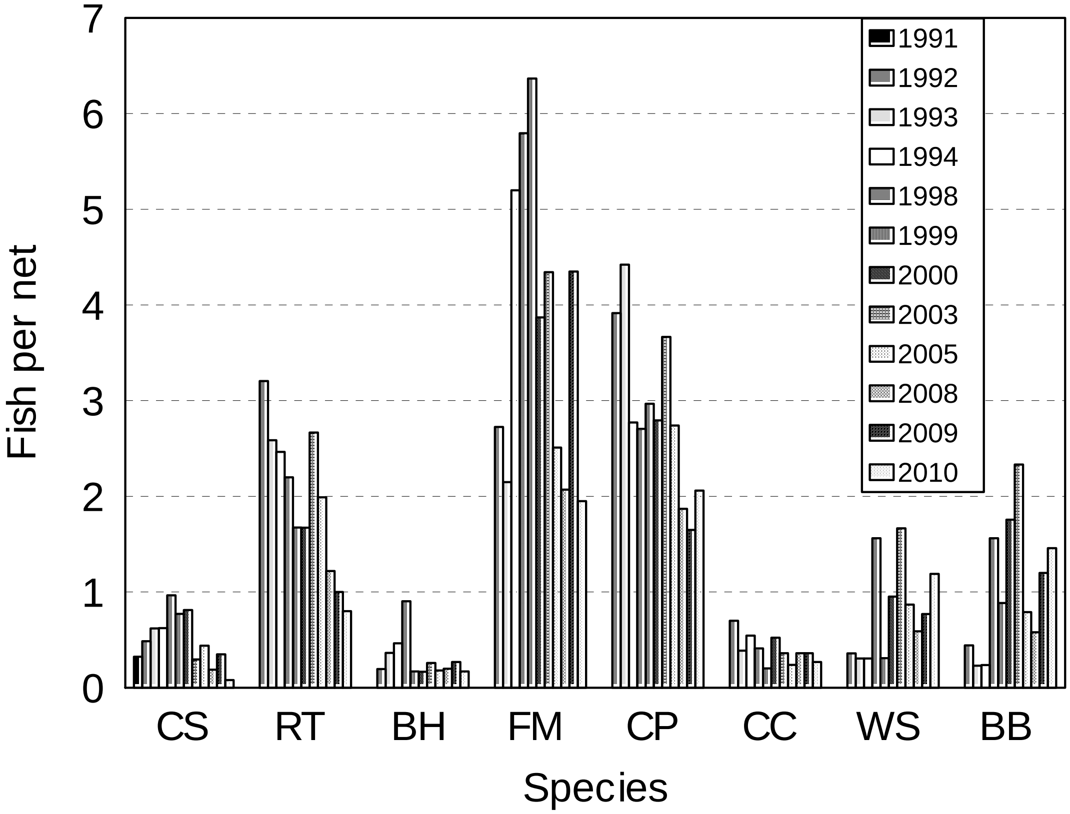

Figure 15. Annual mean trammel-net catch rates (fish/net set) of eight large-bodied fish species in backwaters of the upper-reach study area, 1991-2010. CS: Colorado pikeminmnow; RT: roundtail chub; BH: bluehead sucker; FM: flannelmouth sucker; CP: common carp; CC: channel catfish; WS: white sucker; BB: black bullhead. In 1991, only Colorado pikeminnow were counted.

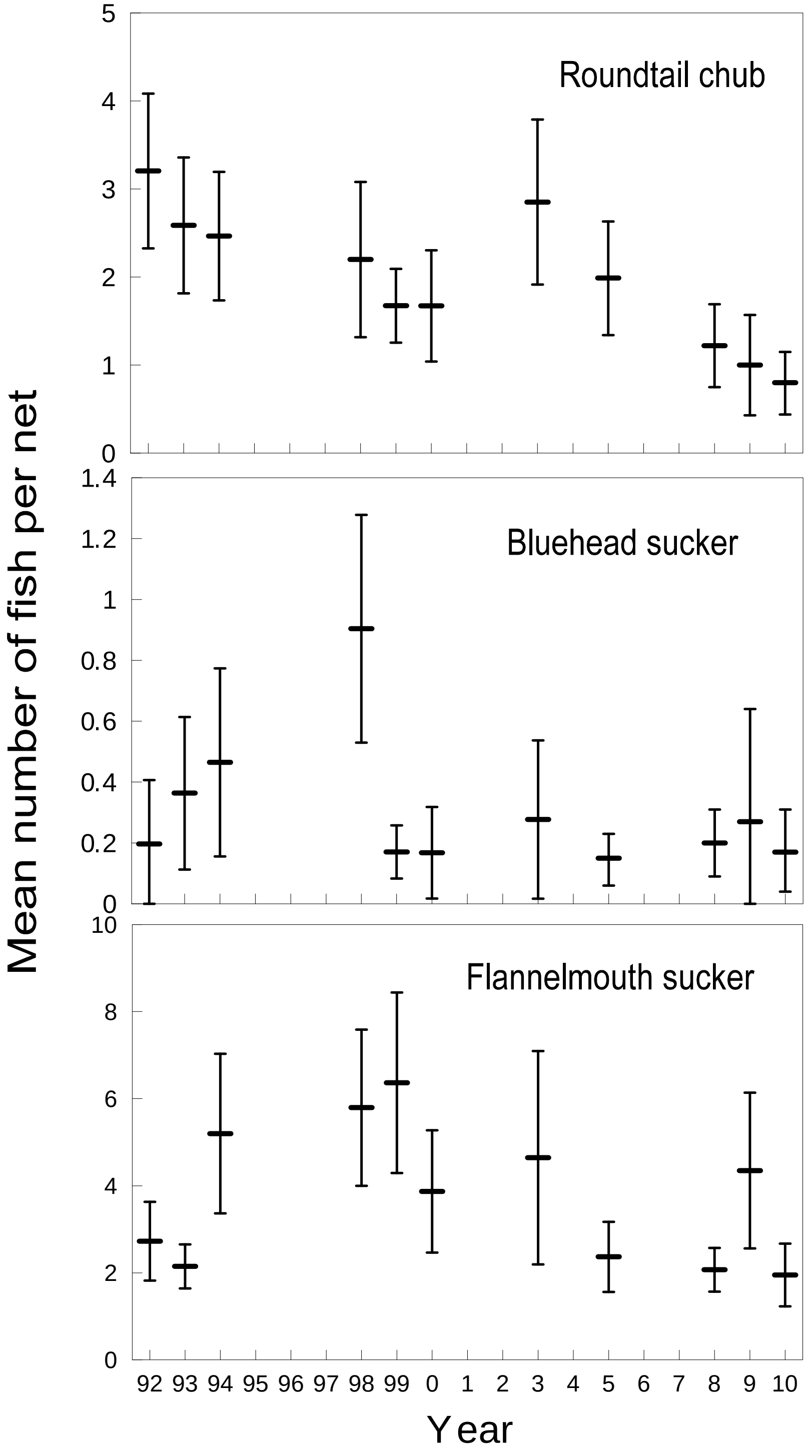

Figure 16. Mean trammel-net catch rates (fish/net set) of native fish species captured from zero-velocity habitats in the upper-reach study area, 1992–2010. Error bars represent the 95% confidence interval.

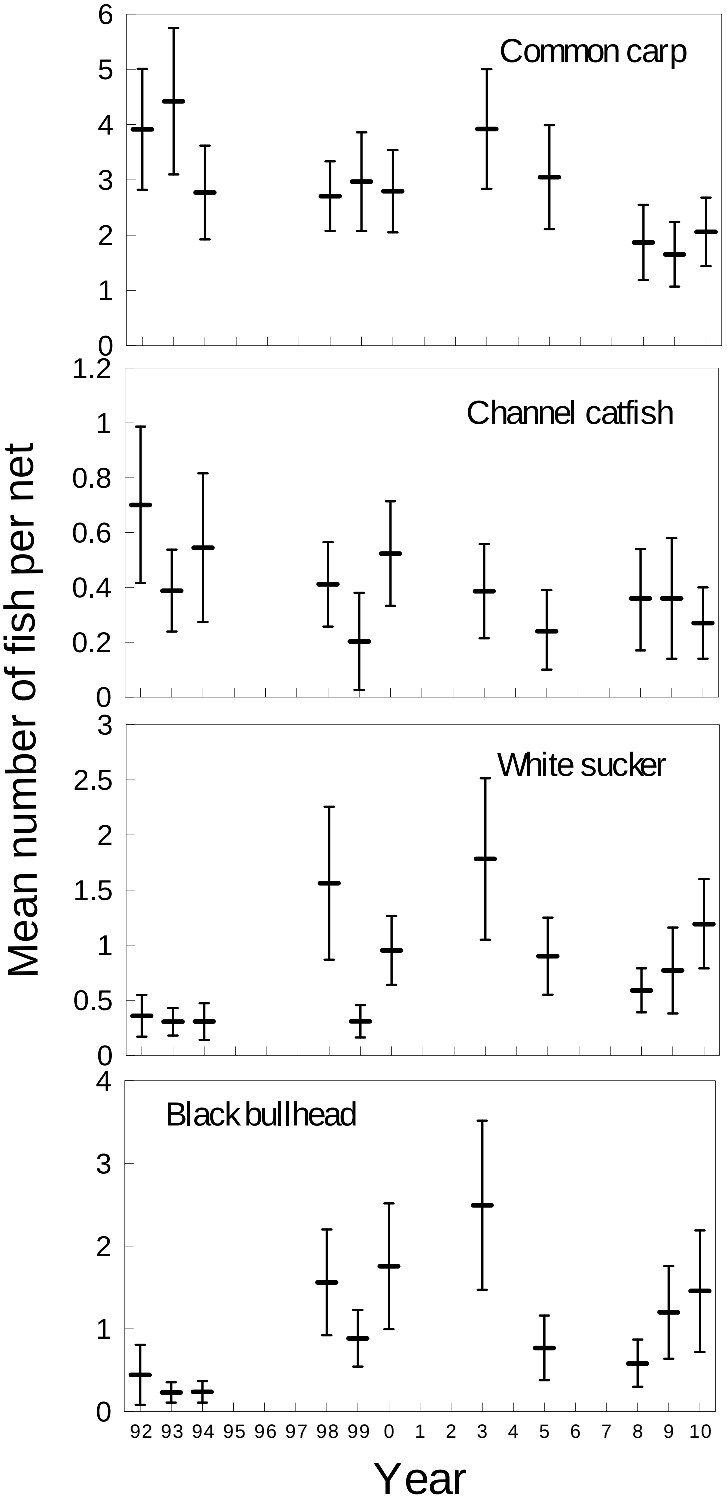

Figure 17. Mean trammel-net catch rates (fish/net set) of non-native fish species captured from zero-velocity habitats in the upper-reach study area, 1992–2010. Error bars represent the 95% confidence interval.

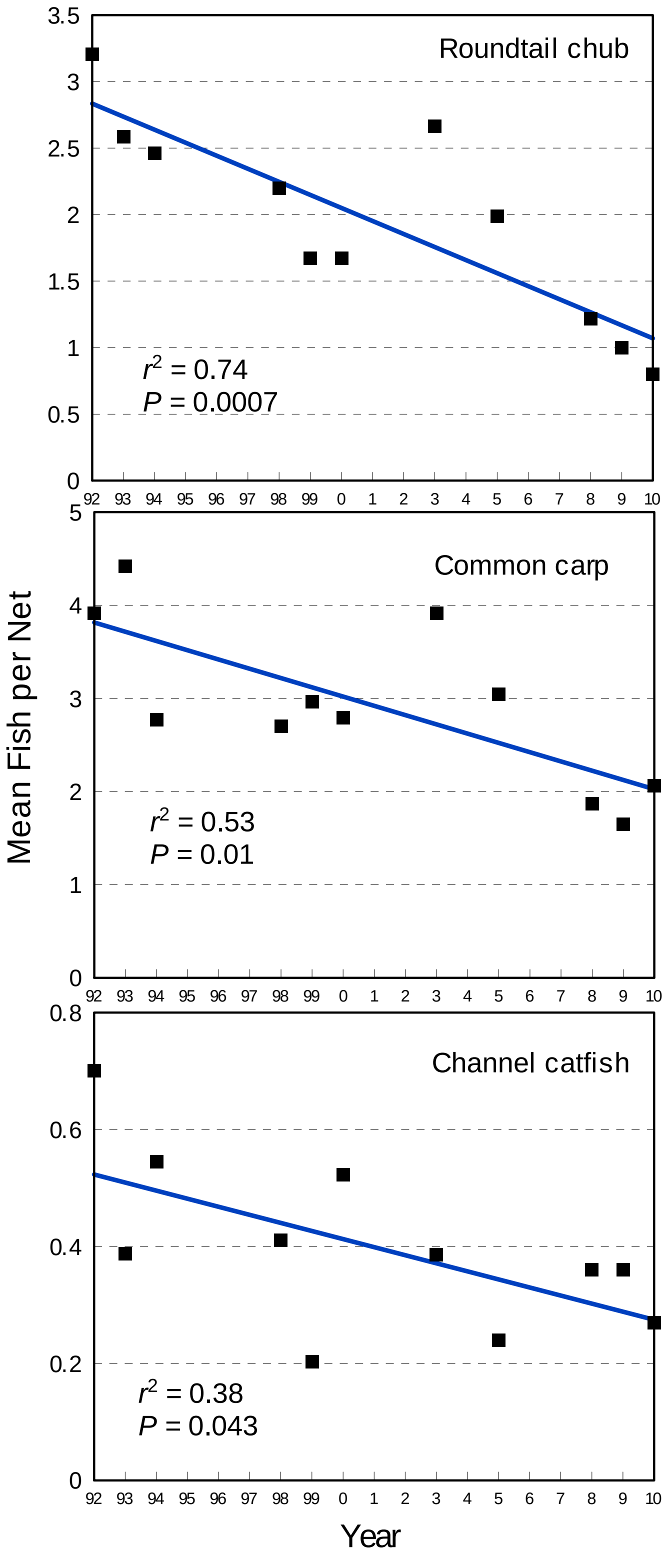

Figure 18. Linear regression of trammel-net catch rates in the upper-reach study area and year of capture. Only those species with significant relationships are shown. Insufficient trammel-netting was done in 2004 to develop means. Numbers of sympatric species were not recorded in 1991.

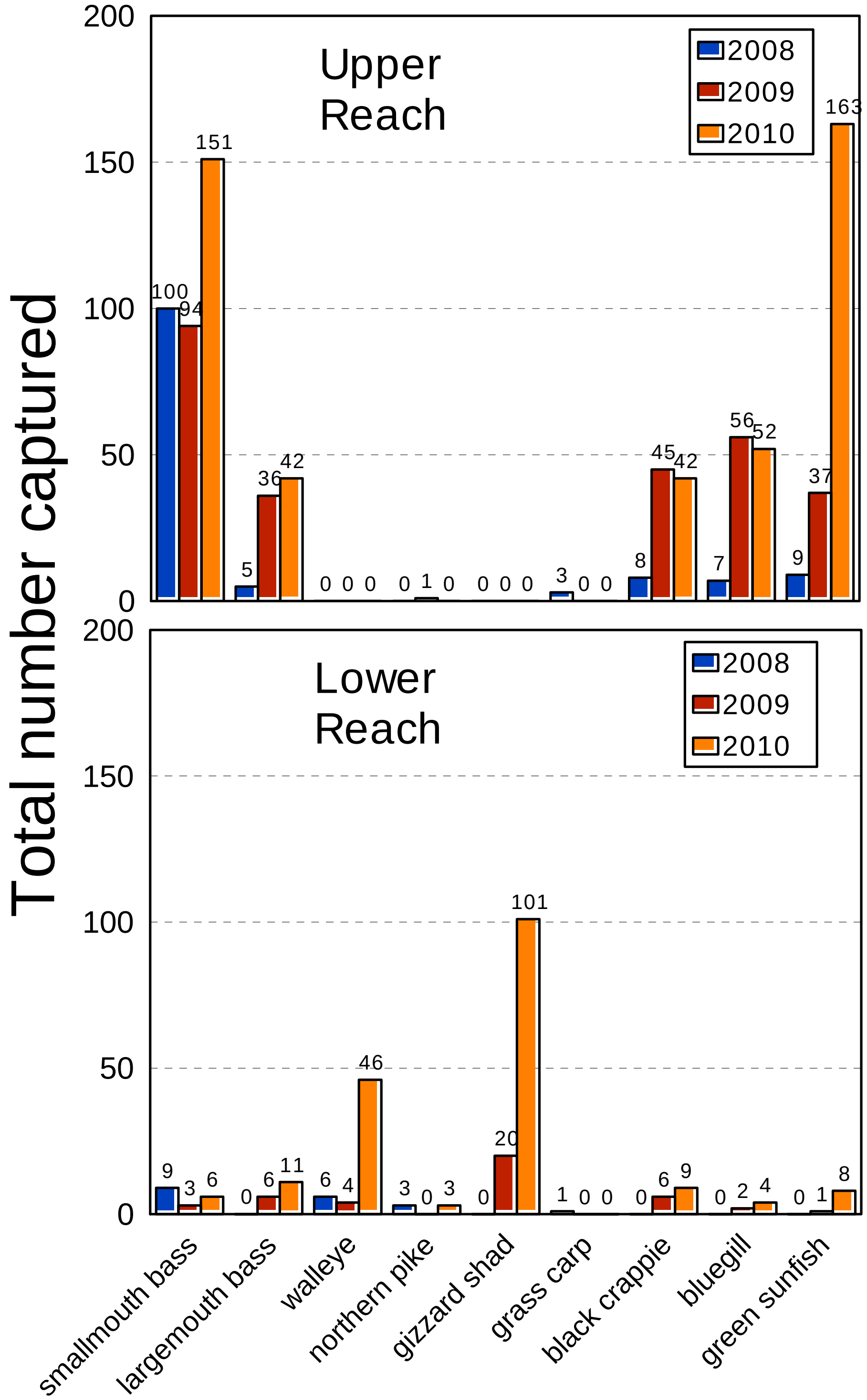

Figure 19. Non-native fish captured during April-June sampling for Colorado pikeminnow in the Colorado River, 2008-2010. Carp, white sucker, channel catfish and black bullhead are not shown. Sampling included both electrofishing and trammel netting. Bars represent total number captured rather than catch rates.

Northern pike and grass carp remained rare throughout the study area. Captures of walleye, perhaps the closest ecological equivalent to Colorado pikeminnow, had been relatively rare in the lower reach (2008: 6; 2009: 4), but then increased substantially in 2010 when 46 individuals were captured (and removed) between RM 12 and 71.

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).

Years 2003–2005. — In the upper reach, fish < 450 mm TL comprised 0–5% of the sampled population during all four study periods, indicating few fish in the upper reach were reared there. When individuals moved from the lower reach to the upper reach, most evidently did so only after having reached a length > 450 mm TL. This is supported by the size of fish captured in the lower reach one year and recaptured in the upper reach the following year (refer to Table 6). In the upper reach, few young adults were captured in 2003: only 4% of the sample was < 550 mm TL and none were < 500 mm TL (not shown; see Osmundson and White 2009). Hence, evidence of recent dispersal to the upper reach was minimal. In 2004, 7% of the sample was < 500 mm TL perhaps representing the first upstream migrants of the large cohort observed in the lower reach in 2003 (1998 year class). By 2005, fish < 500 mm TL comprised 29% of the upper reach sample.

Years 2008–2010. — In the upper reach, almost all fish captured during 2008–2010 were ≥ 500 mm TL (Figure 20). 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 (see Table 6).

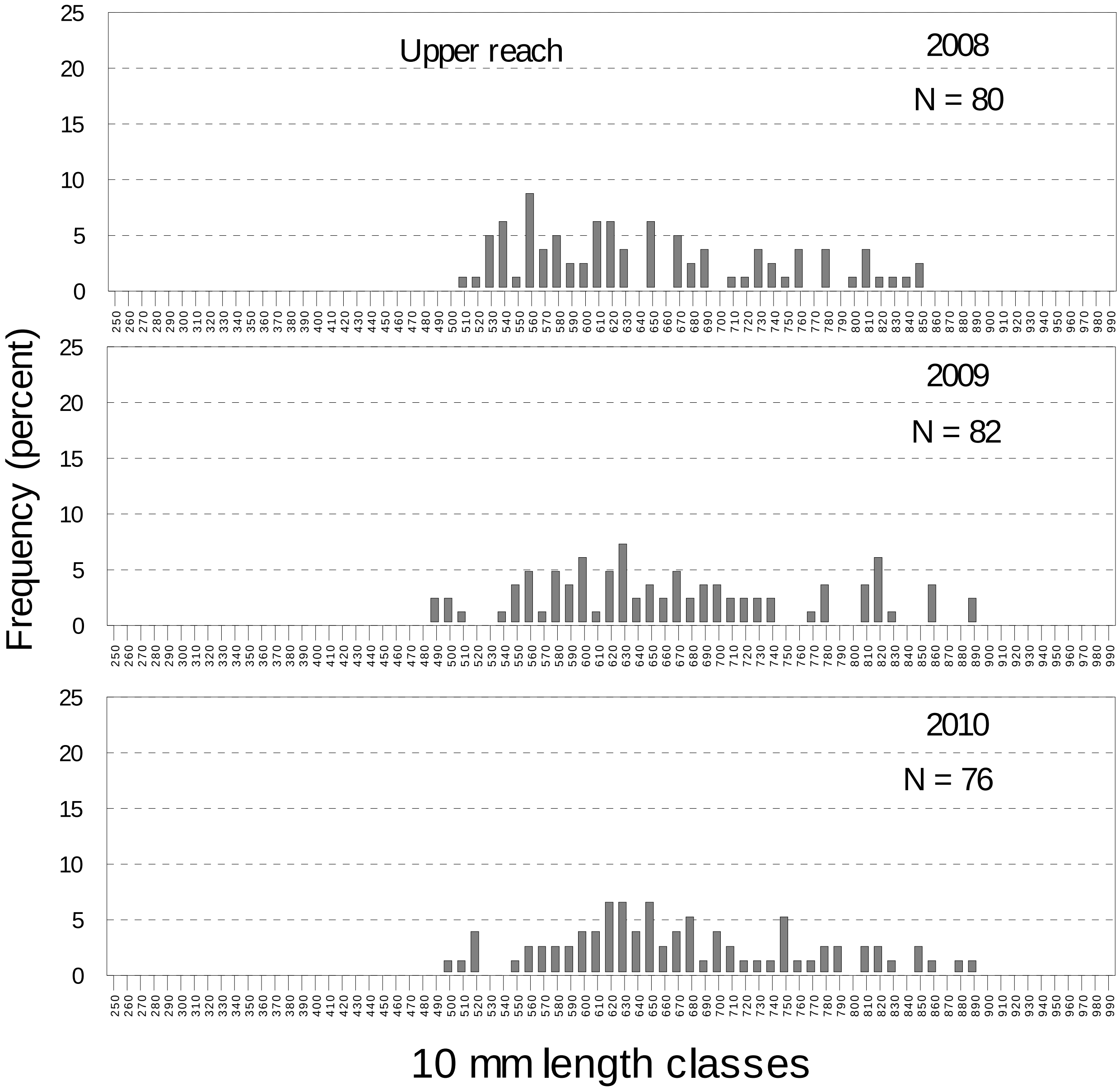

Figure 20. Length frequencies of Colorado pikeminnow captured in the upper Colorado River study reach, 2008–2010.

Relative abundance of large adults. – There were more large adults captured in the lower reach during 2003–2005 and 2008-2010 than in the early 1990s. During 1991–1994, individuals > 650 mm TL made up 0–2% of the sample; during 1998–2000, 0–8%. During 2003–2005, large adults made up 5–12% of the sample; during 2008-2010, 8-10%.

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%). Growth of the strong and moderately-strong year classes produced during 1985–1987 likely contributed to the increased percentage of larger fish. During 2008–2010, the percentage of fish > 650 mm TL in the upper reach was 46-57%. The percentage of adults captured that were very large and old (≥ 800 mm TL) varied substantially 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%.

Recruitment Indices

Temporal variation in median length – A decline in the median length of adults in the upper reach was first observed in the early 1990s (Figure 21), 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. 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 2010, suggesting that upstream movement of young adults to the upper

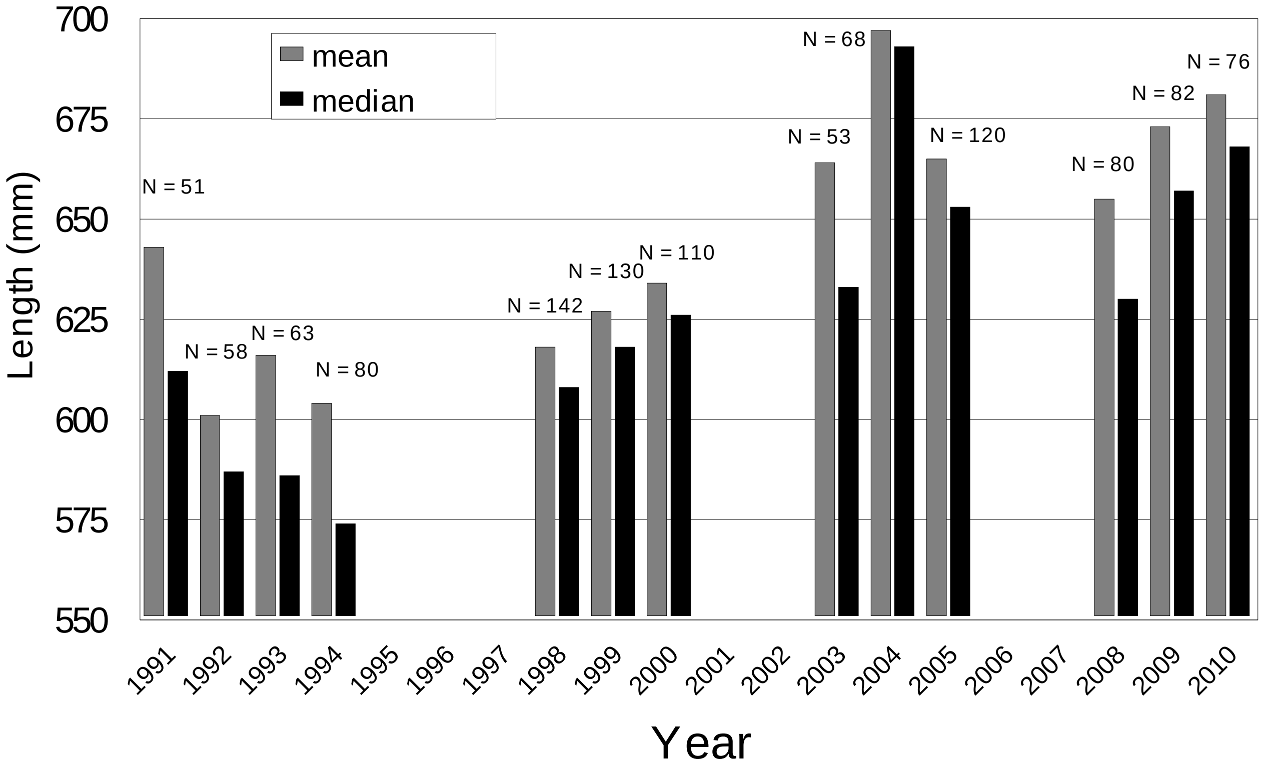

Figure 21. Mean and median lengths of Colorado pikeminnow captured in the upper Colorado River study reach, 1991–2010. N = sample size.

reach had tapered off. Trends in median lengths indicated there may have been only two strong year-classes (1986 and 1998) with origins between 1985 and 2005.

Relative year-class strength. – Relative strength or weakness of other year classes not producing an obvious change in median length was more difficult to determine. For these year-classes, the relative abundance at age-5, detected from length frequencies in the lower reach, was the best indication of cohort strength. However, during non-sampled years, relative abundance at age-5 could not be assessed, so relative abundance at age-4, age-6 or age-7 was qualitatively assessed from histograms derived from the most recent or subsequent sampling years. Results for years assessed using age-5 fish are reported here first.

In 1991, fish estimated to be age-5 made up 76% of the sample captured from the lower reach (Figure 22; Table 8). 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

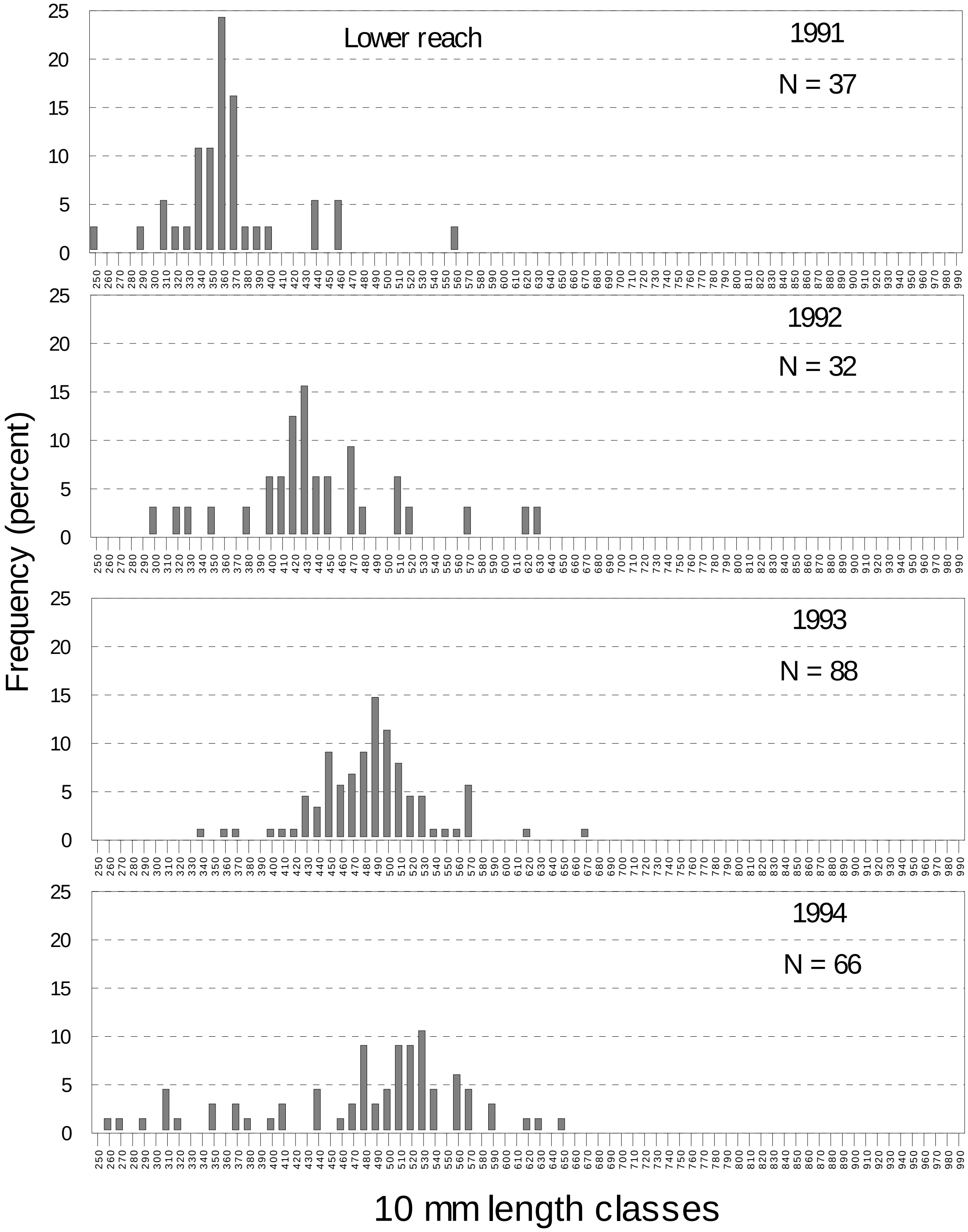

Figure 22. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 1991–1994.

Table 8. 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 and 2008–2010. 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

[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.

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 23). 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 recommenced 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 24). 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 25). 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)

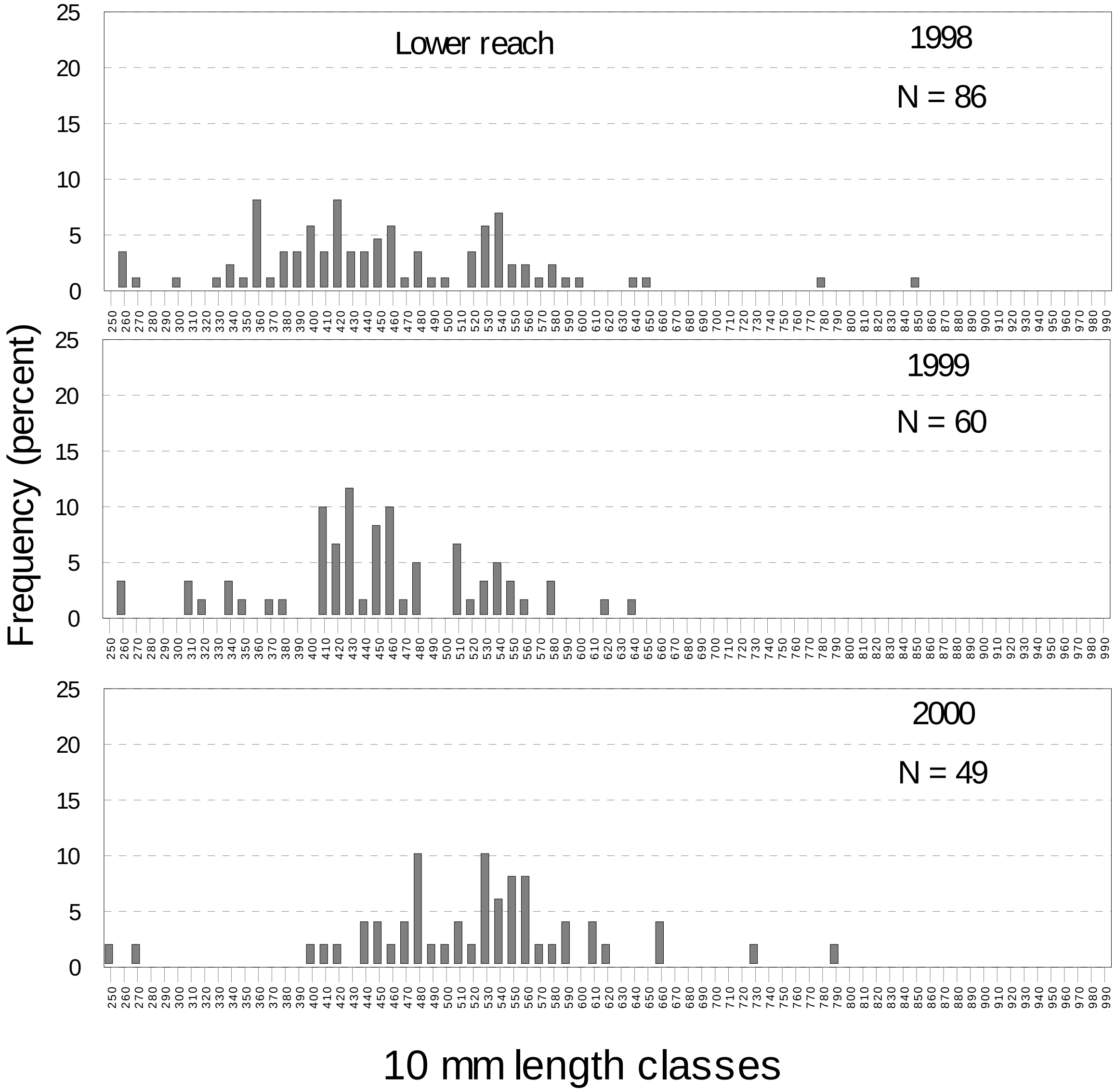

Figure 23. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 1998–2000.

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 25) and 2005 therefore ranked as a year class of moderate strength.

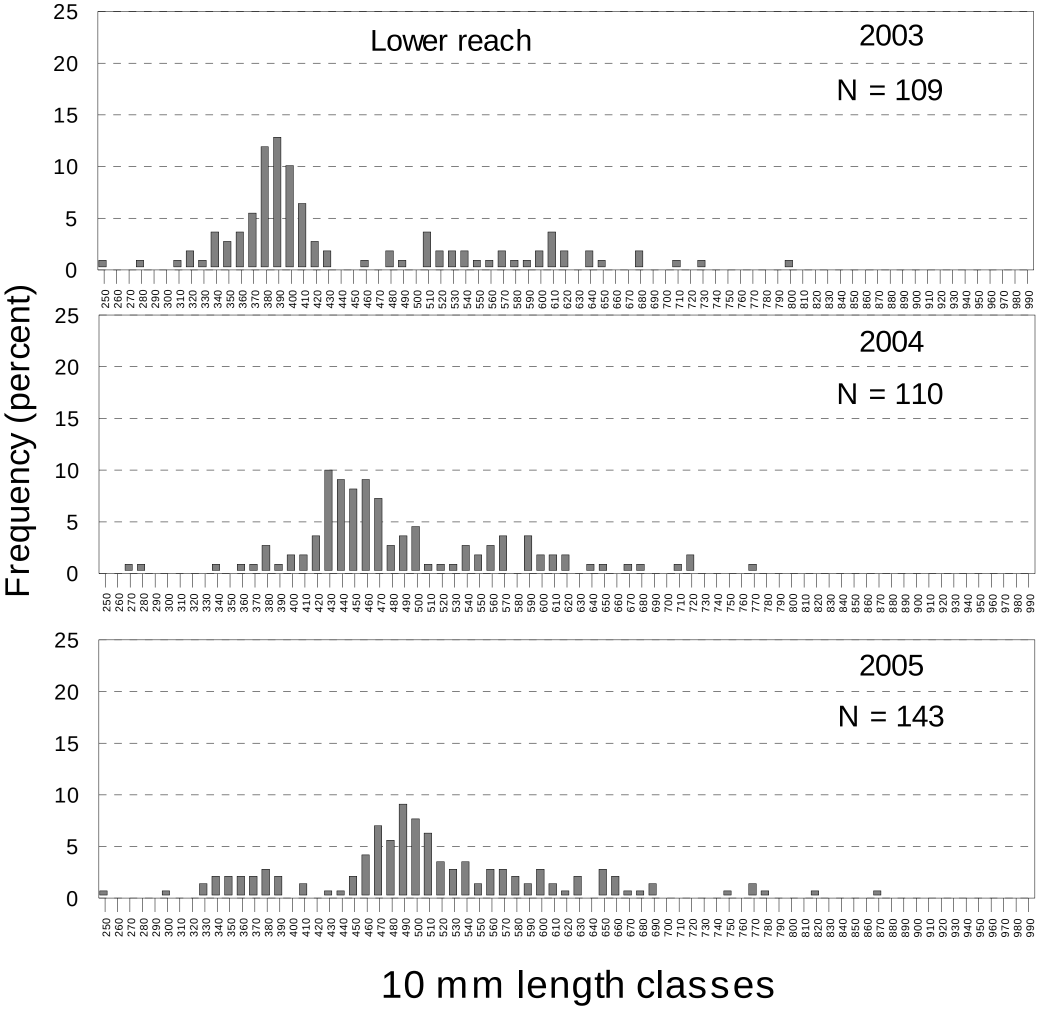

Figure 24. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 2003–2005.

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,

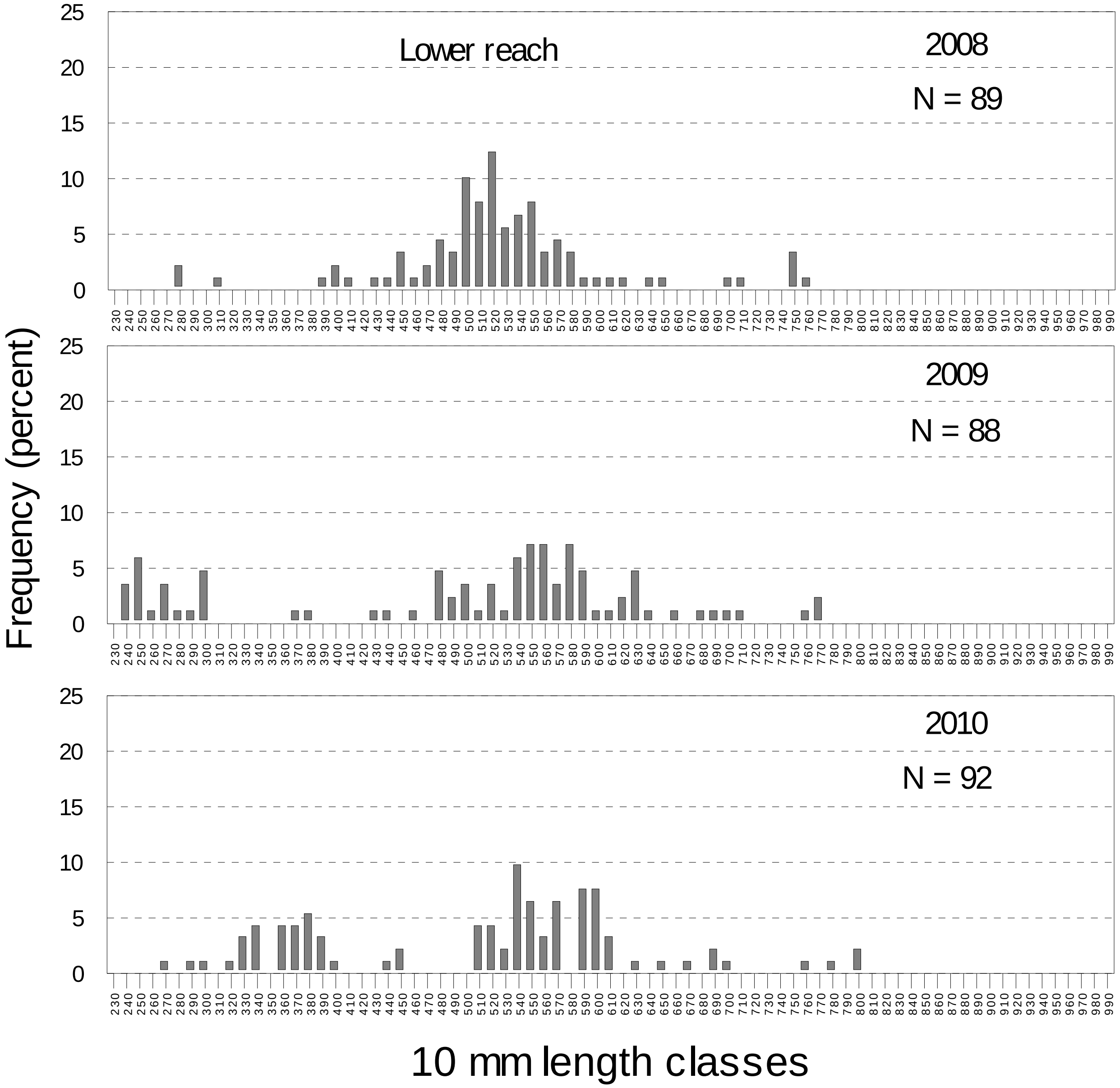

Figure 25. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 2008–2010.

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. Also, 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.

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 12 weak, six moderate, and only two strong year classes produced between 1986 and 2005 (Table 8).

Year-class Strength at Age-5 in Relation to Strength at Age-0

We examine here whether there is linkage between high catch rates of young fish in fall of their first year and high catch rates of juveniles 4–6 years later. From 1986 to 2010, there were three years with relatively high catch rates of YOY in the lower reach: 1986, 1996, and 2009 (Figure 26). The nine intervening years between 1986 and 1996 could be characterized as all having moderate levels of YOY abundance. Curiously, subsequent to 1996, relative abundance appeared to fall off fairly dramatically. Aside from a high catch

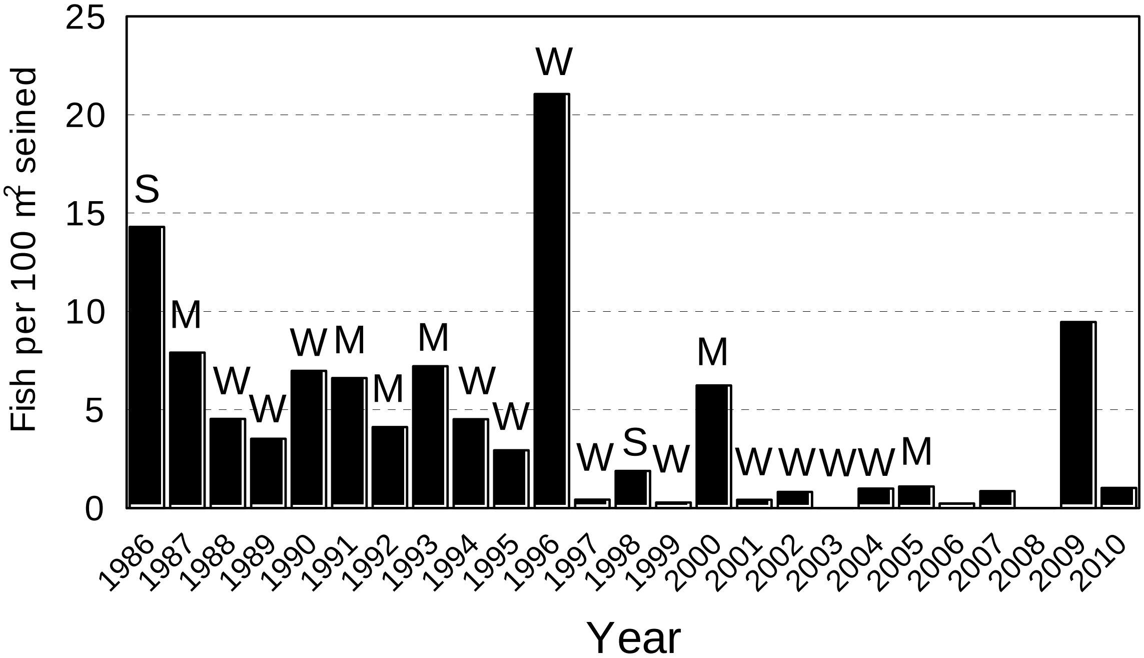

Figure 26. Catch-per-unit-effort of young-of-the-year Colorado pikeminnow seined from Colorado River backwaters, 1986–2010 (data from Breen et al. 2011), and the later strength of the corresponding year class at age-5 (see Table 7). S = strong, M = moderate, and W = weak (at age-5). Strength at age-5 cannot yet be assessed for year classes of 2006–2010.

rate in 2009, relative abundance was of moderate strength in only one year (2000) and was weak in 12 others. No YOY at all were captured in two of the weak years.

There was agreement between the relatively high catch rates of YOY in 1986 and our assessment of strength of that year class at age-5 (i.e., it was strong at age-0 and at age-5). After this, fall YOY catch-per-unit-effort (CPUE) was a less useful index for predicting strength at age-5, and perhaps later adult recruitment. Most noteworthy was the change in strength of the 1996 year class: it began exceptionally strong in fall 1996 but then essentially disappeared by age-5. Of the nine moderately strong year classes at the YOY stage between 1986 and 1996, only four remained moderately strong until age-5; the rest became weak. Of the nine years following 1996, one year class (2000) began moderately strong and remained so at age-5; six year classes began weak and remained weak, two year classes began weak but were of moderate strength by age-5. Finally, the 1998 year class began weak, but by 2003, appeared to be the strongest pulse of age-5 fish since the 1986 year class in 1991. Strength at age-5 for recent cohorts produced during 2006–2010 cannot yet be assessed. Of the 20 year classes for which we have both YOY CPUE data and a qualitative assessment of strength at age-5, twelve displayed a consistency in relative abundance between age-0 and age-5.

Utilizing a matrix depicting the frequency of observed outcomes (Table 9), the Fisher Exact Test calculated the probability of observing this exact set of outcomes. From the test result ($P = 0.1390$) we could not reject the null hypothesis of independence at the 0.05 alpha level. It is likely there is some relation between year-class strength at the two time periods, but to reject the null hypothesis of independence we would likely need many more years of observed outcomes. The 20 years of outcomes allowed us to estimate the probability that a given year-class strength at age-0 would later result in a given outcome (strength at age-5). Of the nine possible outcome combinations, a weak year class remaining weak had the highest probability at 75.0% (95% CI = 0.41-0.95). However, for the other possible outcomes, the probabilities and associated 95% confidence intervals suggest that year-class strength at age-0 provides little predictive power. For instance, we can estimate only a 50% probability that an initially strong year class will remain strong until age-5. In addition, because the estimate is based on a relatively small set of observed outcomes, we can state with 95% confidence only that the probability is between 3.8% and 96.2% (Table 10).

Table 9. Observed frequencies of possible outcomes from comparisons between strength of year-classes at age-0 and at age-5 for Colorado pikeminnow in the lower-reach of the Colorado River study area (1986–2005). Fall, young-of-the-year, seining catch rate was used as the basis for strength at age-0; relative abundance in length-frequency histograms was used as a basis for year-class strength at age-5. For example: for year classes weak at age-0, six were still weak at age-5, one was moderate in strength, and one was strong.

	Age-5			
Age-0	Weak	Moderate	Strong	sum
Weak	6	1	1	8
Moderate	5	5	0	10
Strong	1	0	1	2
sum	11	7	2	20

Table 10. Probabilities of later outcomes (year-class strength at age-5) for each of three year-class strength categories (weak, moderate, strong) for age-0 Colorado pikeminnow in the lower reach of the Colorado River study area. Standard errors (SE) and 95% confidence intervals (CI) are also shown.

Age-0	Age-5	Estimate	SE	95% CI
Weak	Weak	0.750	0.153	0.408–0.953
Weak	Moderate	0.125	0.117	0.008–0.446
Weak	Strong	0.125	0.117	0.008–0.446
Moderate	Weak	0.500	0.158	0.217–0.783
Moderate	Moderate	0.500	0.158	0.217–0.783
Moderate	Strong	0.000	0.000	0.000–0.176
Strong	Weak	0.500	0.354	0.038–0.962
Strong	Moderate	0.000	0.000	0.000–0.622
Strong	Strong	0.500	0.354	0.038–0.962

Body Condition

Differences among length classes. — In the lower reach, mean relative body condition (K_n) was significantly lower for those Colorado pikeminnow 500–599 mm TL than it was for those 400–499 mm TL in all four sampling periods (Figure 27-bottom). Similarly, mean K_n was lower for fish 600–699 mm TL than for those 500–599 mm TL, but differences were significant in only one of the three sampling periods (2003–2005). Differences among other 100-mm length classes were mixed: Colorado pikeminnow 300–399 mm TL had lower mean K_n than those 200–299 mm TL in two periods, higher in one period, and essentially the same in one period. Mean K_n of those 400–499 mm TL was significantly less than that of those 300–399 mm TL in two periods but essentially equal in two other periods.

In the upper reach, mean K_n generally increased with fish length (up to 800 mm TL) in all four sampling periods, though differences among 100-mm length classes were not always significant (Figure 27-top). During the 2008–2010 sampling period, only two individuals in the 400–499 mm length class were captured, so comparisons in mean K_n between this and greater length classes could not be made. Mean K_n of fish 800–899 mm TL was lower than that of fish 700–799 mm TL in two periods but slightly higher in two other periods; however, none of the differences were statistically significant.

Differences among periods. — Mean K_n of almost all 100-mm length-classes in the lower reach declined significantly between the first (1991–1994) and second sampling periods (1998–2000). However, by the third sampling period (2003–2005) mean K_n had increased and was again as high or higher than in the first sampling period (Figure 27-bottom). Most of the significant differences among periods were for three length-classes: 300–399 mm, 400–499 mm, and 500–599 mm TL; differences in mean K_n among periods for fish 200–299 mm and fish 600–699 mm TL were not significant (likely due to small sample sizes). In the fourth and most recent period, mean K_n of lower-reach Colorado pikeminnow of two length classes (300–399 and 500–599 mm TL) was significantly lower than during the first and third sampling periods. For the 300–399 mm group, mean K_n was, however, significantly higher than in the second sampling period (1998–2000). Differences among periods for other length classes were not significant.

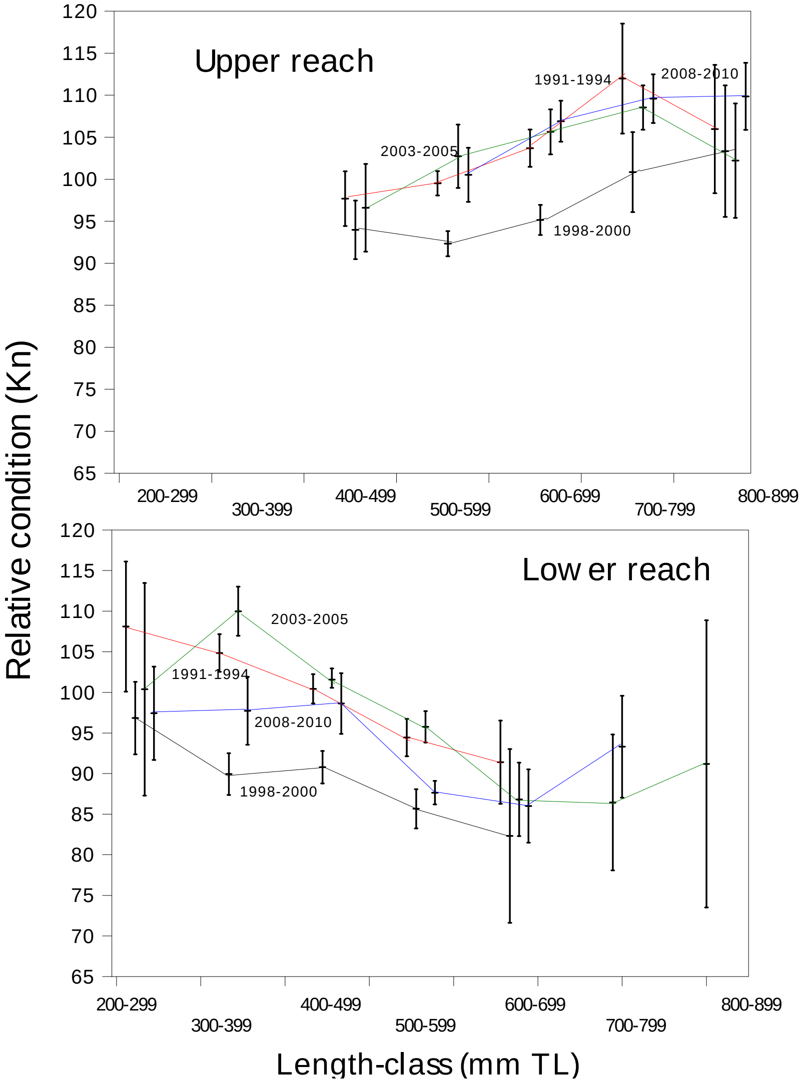

Figure 27. Mean relative body condition (K_n) of Colorado pikeminnow in the upper and lower reaches of the Colorado River study area during four sampling periods, 1991–1994, 1998–2000, 2003–2005, and 2008–2010. Means are for seven 100-mm length classes. Data from all years within each multi-year period were pooled before calculating means. Upper and lower bars represent 95% confidence intervals.

A similar pattern was observed in the upper reach: for three length-classes (500–599 mm, 600–699 mm, and 700–799 mm TL), mean K_n significantly declined between the first and second periods, followed by a significant increase in mean K_n by the third sampling period (Figure 27-top). However, differences in mean K_n among periods for two 100-mm length classes (400–499 mm and 800–899 mm TL) were small and not significant. Mean K_n

in the most recent period (2008–2010) was very similar to that in the first and third periods for all length groups with adequate samples to plot.

Differences among years. — To simplify monitoring mean K_n through time, the 500–599 mm length class was used as an index for making among-year comparisons. In the lower reach, mean K_n of fish 500–599 mm TL was similar among years within the first sampling period (Figure 28-bottom). However, mean K_n then apparently declined sometime during the subsequent three non-sampling years. When fish were again sampled in 1998, mean K_n was the lowest of any sampled year. During the next two years, mean K_n progressively

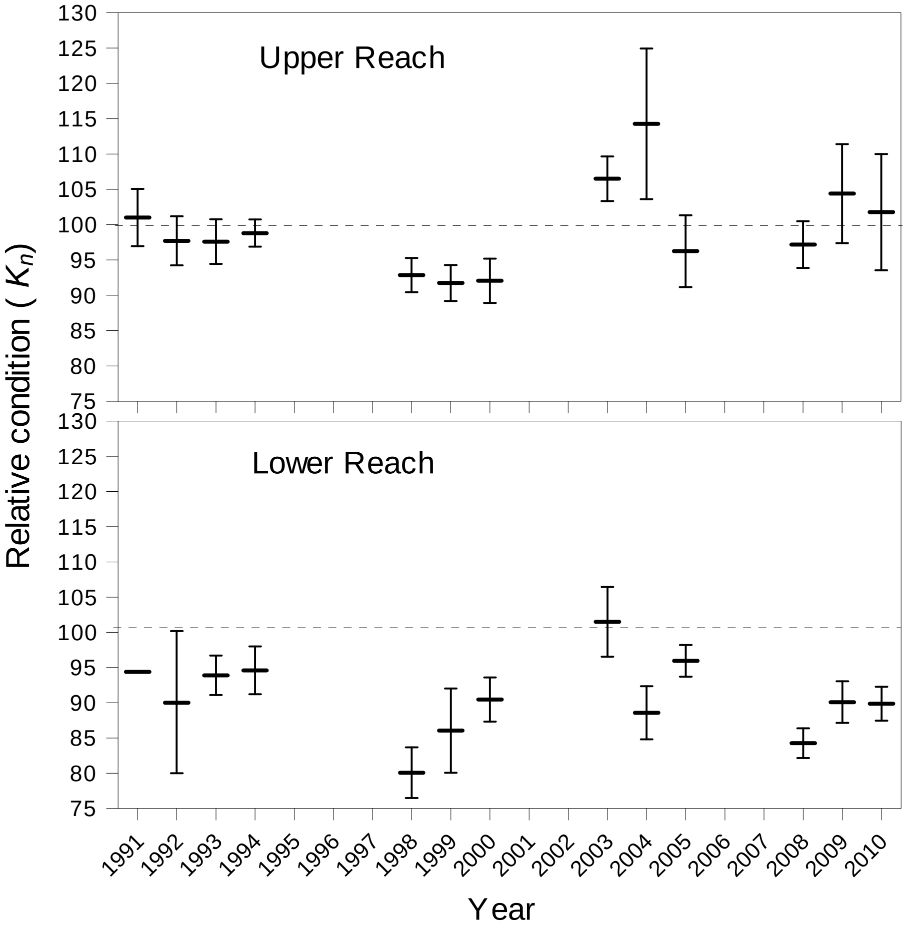

Figure 28. Mean relative body condition (K_n) of Colorado pikeminnow 500–599 mm TL by year in the upper and lower reaches of the Colorado River study area. Dashed horizontal lines at $K_n = 100$ represent the average relative body condition for the population calculated from all fish captured during 1991–1994. Error bars represent the 95% confidence interval.

increased; by 2000 it was significantly higher than in 1998. This upward trend may have continued through the next two non-sampling years (2001 and 2002) because by 2003 mean K_n was at the highest level of any sampling year. However, mean K_n then underwent several changes in direction, significantly decreasing between 2003 and 2004, significantly increasing between 2004 and 2005, significantly decreasing between 2005 and 2008, and significantly increasing from 2008 to 2009. Between 2009 and 2010 mean K_n was essentially unchanged. Hence, with the exception of the first sampling period and the last two years, mean K_n for this length class was highly variable among years.

In the upper reach, mean K_n of fish 500–599 mm TL was also similar among the first four years of sampling (Figure 28-top). Between 1994 and 1998 it significantly declined and then remained stable through 2000. However, when fish were again sampled in 2003, mean K_n was significantly higher. During 2003 and 2004, mean K_n was at the highest levels observed. However, in 2005 and 2008 mean K_n was significantly lower and had returned to levels similar to the first sampling period. Finally, mean K_n may have increased in 2009 and 2010, but differences were not significant.

Differences between reaches. — There was some consistency in body condition dynamics between the upper and lower reaches for the 500–599 mm length-class. For instance, in both reaches mean K_n was fairly stable during 1991–1994, it decreased between 1994 and 1998, and it increased between 2000 and 2003. By 2005, mean K_n in both sub-reaches had returned to levels very similar to those during the first sampling period. Fish of the two reaches did, however, exhibit some dissimilarity in the direction of year-to-year changes. For instance, while body condition remained fairly stable in the upper reach during 1998–2000, it steadily increased in the lower reach. Also, mean K_n significantly decreased from 2003 to 2004, then increased from 2004 to 2005 in the lower reach while it appeared to do just the opposite in the upper reach. Finally, mean K_n significantly declined between 2005 and 2008 in the lower reach while it remained unchanged in the upper reach.

Relations with abundance. — There was a very slight negative, non-significant relationship ($r^2 = 0.127$; $P = 0.23$) between our annual, upper-reach abundance point estimates of Colorado pikeminnow $\geq$ 500 mm TL and annual mean K_n of fish $\geq$ 500 mm TL from the upper reach (i.e., as abundance increased, mean condition declined). In the lower reach, there was a slight positive, non-significant relationship ($r^2 = 0.28$; $P = 0.08$) between abundance point estimates and annual mean K_n for fish $\geq$ 500 mm TL (i.e., as abundance increased, mean condition improved).

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 2010, there was a total of 14,662 captures reported (including recaptures) in the upper-basin of Colorado pikeminnow that were PIT-tagged at the time of capture or previously (Table 11). These included 3,585 captures (1,912 different fish) in the Colorado River system and 11,077 captures (7,709 different fish) in the Green River system. To discern whether a fish made an inter-system movement, at least two captures of a fish must be made. By the end of 2010, there was a total of 2,976 PIT-tagged fish in the upper basin database with multi-capture histories (two or more captures, excluding those recaptures that occurred in the same day): 773 individuals first captured and tagged in the Colorado system and 2,203 individuals similarly captured in the Green River system. Hence, 40% of the unique Colorado-River-captured fish were recaptured at least once and 29% of the Green-River-captured fish were recaptured.

During 1991–2010, there were 54 documented inter-system movements (Appendix Table VII). Thirteen of these capture-recapture events were one year apart; another 15 such events were two years apart. Only once did the recapture occur in the same year as the preceding capture (one month apart). The greatest elapsed time between captures was nine years. Some of the fish may have been sub- or young adults when the movement occurred, but most (30 fish) were $\geq$ 500 mm TL when last captured before moving to the other river system. Two fish were > 700 mm TL before they moved.

Rather than moving short distances into the adjacent river from locations near the confluence of the Green and Colorado Rivers, many of these fish moved relatively long distances. Eight fish moved over 400 miles (644 km) between captures, and one fish moved from the Gunnison River to the Green River and then back to the Colorado River for a total of 887 miles (1,427 km) in a three-year period. Twenty-one of 27 (78%) fish that moved from the Colorado system were tagged and last captured in the Colorado River within 70

Table 11. Total number of Colorado pikeminnow captures in upper basin rivers since use of PIT tags began, 1990-2010. Values do not represent number of different fish captured, rather the number of captures, including recaptures. 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 2.2). Capture records for 2004 and 2005 in the Colorado River do not include the capture of recently stocked fish.

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**
Total	**3,284**	**298**	**3**	**7,975**	**1,595**	**1,400**	**76**	**21**	**7**	**3**	**14,659**

[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

miles (113 km) of the confluence, whereas only 11 of 27 (41%) fish that moved out of the Green River were tagged and last captured within 70 miles of the confluence. Thirteen of the 48 (27%) unique fish that made inter-system movements first did so from locations at least 100 miles (161 km) upstream of the confluence.

All fish that moved to the Colorado River system were previously caught in the Green River mainstem (not in a tributary). Most (77%) fish that moved from the Colorado River system were next captured in the Green River mainstem, but not all; some were next caught in tributaries: one in the Duschene River; four in the Yampa River; one in the White River. Two fish that moved from the Green River were next caught in the Gunnison River; all others were caught in the mainstem Colorado River.

Of the 2,976 unique, upper-basin Colorado pikeminnow that were captured two or more times, 1.61% had made at least one inter-system movement. Twenty-seven individuals captured in the Colorado River system moved to the Green River system and 27 fish captured in the Green River system moved to the Colorado River system. Six of these fish moved to the other system but later returned; hence, 12 of the 54 inter-system movements were made by six fish. Five of these fish first moved from the Colorado to the Green River system and later returned; one first moved from the Green to the Colorado River system and later returned.

From a numerical standpoint, an equal number of fish are known to have moved from the Colorado River system to the Green River system as those that moved in the opposite direction (27 fish moved to the Green and 27 fish moved to the Colorado); however, on a percentage basis, more of the Colorado River population appeared to be made up of immigrants. Of the 1,912 unique Colorado pikeminnow captured in the Colorado River system, 1.15% had previously been tagged in the Green River system, and of the 7,709 captured in the Green River system, 0.29% had previously been tagged in the Colorado River system. The rate of detected movements from the Green River to the Colorado River over the 19 years of PIT tag captures averaged 1.3 fish per year. In the Colorado River, annual probability of capture averaged 0.22 (Appendix Table II), suggesting total movements from the Green River to the Colorado River averaged 5.9 fish per year.

A higher percentage of Colorado-River-tagged fish emigrated to the Green River system than Green-River-tagged fish emigrated to the Colorado River system. Of 773 fish initially tagged in the Colorado River system and recaptured at least once, 3.4% were recaptured in the Green River system, and of 2,203 fish initially tagged in the Green River system and recaptured at least once, 1.0% were recaptured in the Colorado River system. However, at least five of the fish that moved to the Green River and one fish that moved to the Colorado River later returned to the river they were tagged in. Taking this into account, an estimated 2.7% of Colorado-River-tagged fish emigrated to the Green River system compared to an estimated 1.0% of Green-River-tagged fish that emigrated to the Colorado River system.

Captures of Stocked Colorado Pikeminnow

Some of the 5,084 hatchery-reared Colorado pikeminnow stocked in the Gunnison and Colorado rivers by USFWS and CPW in 2003 and 2004 (Table 12) were captured during the sampling efforts for this study in 2004 and 2005 (previously reported) and in 2008. None of the 2,069 fish stocked in 2003 were later captured. Two Colorado pikeminnow from the 2004 stocking were captured in the lower reach in 2004, and another 22 were captured in Grand Valley canals in 2004 during unrelated fish salvage efforts when canals were drained in late November. In 2005, 45 of the 2004-stocked fish were captured in the study area, five of which were captured twice (50 total captures). Of these, 33 were from the June 1 Gunnison River stocking, twelve from the May 18 Colorado River stocking, and none from the September 15 Colorado River stocking. Nine of the 45 fish were captured in the Grand Valley and 36 were captured in the lower reach. A mark-recapture abundance estimate of these provided an estimate of 190 individuals present in 2005, or 3.7% of those stocked in 2004 and 2005. In 2008, four Colorado pikeminnow from the 2004 stocking were captured in the lower reach. One of these was again recaptured in 2010. No other stocked fish were captured in 2009 or 2010, and none was captured from the upper reach subsequent to 2005. Dividing the number caught in 2008 (four) by the annual probability of capture in the lower reach of wild fish (0.270) provides a rough estimate of 15 hatchery fish still present in the lower reach in 2008, suggesting a 0.3% survival rate of stocked fish after 3-4 years. The number of stocked fish retained in the Colorado and Gunnison rivers upstream of the study area is unknown, but subsequent sampling efforts in both areas have not detected any

Table 12. Colorado pikeminnow stocking information for the Colorado and Gunnison rivers, 2003 and 2004. Abbreviations: RM = river mile; FWS = U.S. Fish and Wildlife Service; CPW = Colorado Parks and Wildlife.

Stocking Date	**Agency**	**River**	**RM location**	**Number stocked**	**Mean length (mm)**	**Length range (mm)**
			2003			
Apr 14	FWS	Colorado	167.7	12	120	100–140
Oct 10	FWS	Gunnison	57.1	1,048	242	116–311
Nov 06	FWS	Colorado	216.6	1,001	222	152–350
Total				**2,069**		
			2004			
May 18	CPW	Colorado	240.7	1,164	184	134–292
Jun 01	CPW	Gunnison	57.0	1,200	217	142–270
Sep 15	CPW	Colorado	240.7	651	204	150–235
Total				**3,015**		

(USFWS unpublished data). Colorado pikeminnow identified as stocked fish were not included in the capture-history matrix of wild fish, and abundance estimates of stocked fish in the study area were not added to the mark-recapture estimates of wild fish.

DISCUSSION

Wild, self-sustaining populations of Colorado pikeminnow are currently restricted to two primary river systems in the upper Colorado River Basin: the Green and Colorado. The two populations are likely genetically linked through annual exchange of a small number of adults. However, demographic dynamics of each population appear to behave independently of one another. Trends from electrofishing catch-rate monitoring during 1986-2000 (McAda et al. 2002), coupled with mark-recapture abundance estimation monitoring during 1991-2010 (this study), indicated very low abundance in the Colorado River mainstem population through about 1991, when there were perhaps as few as 200 adults remaining upstream of the Green River confluence (Osmundson and White 2009). Strong and moderately strong year classes originating in the mid-1980s (1986-1987) resulted in significant recruitment that essentially rescued this population from gradual extirpation. Beginning in 1991, catch rates increased and the first river-wide abundance estimate in 1992 indicated a population level of 440 individuals $\geq$ 450 mm TL. Additional recruitment from a few moderately strong year classes likely hatched during 1991-1993, followed by a strong year class believed hatched in 1998, resulted in the population reaching a peak in abundance by 2005 with an estimated 889 individuals. Numbers of fish $\geq$ 450 mm TL declined after this point and were estimated at 511 in 2009 and 493 in 2010. Annual fall seine monitoring of lower-reach backwaters during 1986-2010 (summarized by Breen et al. 2011) indicated an abrupt reduction in densities of young-of-the-year Colorado pikeminnow following 1996, suggesting either a decline in spawning success or increased mortality rates of early life stages. This, in addition to an estimated decline in adult survival rate, documented here, raise concerns of whether limited recruitment events can keep pace with adult mortality rates, and ultimately the prospects for self-sustainability of this population over the long term. Below we discuss specific results of the mark-recapture studies and attempt to integrate these findings with those from other studies so that demographics and prospects for recovery of this population can be viewed and understood in a broader context.

Model Selection

Model selection results using the new 2004–2010 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. 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. During 2004 to 2010 there were very few documented movements and 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 significant decline in capture probability from the first half (1991–1998) of the long-term study period to the second half (2003–2010) is noteworthy. The reduction appeared to occur abruptly between year 2000 and 2003. 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 of the study period. 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. One of the sites, a connected pond at Walker State Wildlife Area, had often yielded numerous Colorado pikeminnow with each pass. 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: 1) survival rate was significantly lower in the lower reach than in the upper reach during the most recent period (2008–2010), and 2) there appeared to be a trend of declining survival rate over time in the lower reach. 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 (≥ 250 mm TL) and were not specific, as before, to that of adult fish (≥ 500 mm TL). This would have little effect on the upper-reach survival rate estimate because almost all fish there were ≥ 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 small Colorado pikeminnow. Hence, 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 88.4% in the upper reach and 72.7% in the lower reach can be compared with the results of Bestgen et al. (2007) and Bestgen et al. (2010) 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 and 80% during 2006–2008. 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. Over the entire study period (1991–2010), 23 of the 27 tagged Colorado pikeminnow that moved from the Colorado to the Green River system were last captured in the lower reach of the Colorado River study area before emigrating. Hence, some part of the difference in ‘apparent’ survival between the lower and upper reaches is likely due to unequal emigration rates. We currently can offer no explanation for why actual lower-reach mortality might be higher than upper-reach mortality.

Declining survival rate in the lower reach, if real, is cause for concern. Again, part of the reason why the recent survival rate was lower in the lower reach than during previous periods can be explained by the inclusion of younger, smaller individuals in the estimate. However, survival rates (individuals ≥ 500 mm TL) during the three previous sampling periods also suggested a decline. Those survival rate estimates had fairly large, overlapping confidence intervals so it is difficult to conclude there was indeed a decline in survival rate during those years. If the population is to remain self-sustaining, any real decline in survival rate must be balanced by an increase in recruitment rate – something that was evidently not occurring during the recent sampling period. In the future, an expanded capture matrix may again include a length effect on survival. If and when this occurs, an updated survival estimate of just adults ≥ 500 mm TL will provide a better indication of whether survival rates in the lower reach are indeed trending downward.

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 584 (2009) 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 440 (1992) to 889 (2005), with the highest year 2.0 times greater than the lowest year. 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 334 (1992) to 661 (2008) with the highest year 2.0 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, it was 2005; for fish ≥ 500 mm TL, 2008. Declines are affected by the same lag effect: by the time fish ≥ 500 mm TL reached their greatest estimated abundance, the estimate of fish ≥ 450 mm TL had declined by 20%.

Combined-reach abundance estimates of Colorado pikeminnow ≥ 450 mm TL (Recovery Goal adult length criterion) exhibited a positive and significant slope during the first 13 years of the study period (1992–2005), increasing by 102%. This was followed by a 46% decline through the most recent study year (2010), returning to numbers similar to those in 1992 in only five years. So although adult abundance does not fluctuate as dramatically as abundance when younger ages are included, adult 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. 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. 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

In our previous report (Osmundson and White 2009), 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. 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 for which we had data, with a summed net gain of 332 individuals ≥ 450 mm TL. Currently, with the three most recent years added, six of 12 years had an estimated gain in individuals and six years had an estimated loss. The summed net gain since 1992 has shrunk to an estimated 32 fish ≥ 450 mm TL. Although these estimates are imprecise, and gains and losses for some years during the 19-year period could not be estimated, one of the requirements for down-listing outlined in the Recovery Goals (USFWS 2002) for Colorado pikeminnow (i.e., that mean annual recruitment equal or exceed mean annual adult mortality) appears to have been met through the most recent year of study.

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 19 years of study (12 abundance estimates). 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 889 in 2005 dropped to 493 in 2010, a 46% reduction in five 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). Whether a decline has continued during the past two un-sampled years (2011 and 2012) or whether the population has since been ‘rescued’ by a significant recruitment event will determine whether the recent trend remains in a downturn.

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 (Figure 5 and Table 5). 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 transition 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 all of these increases and decreases in annual abundance point estimates were often not statistically significant, they did fit what we might expect given the net transition probabilities.

In addition to perhaps being related to lower-reach population dynamics, the lack of upstream movement from 1998 to 1999 and the negative net upstream movement (more fish moving downstream than upstream) from 1999 to 2000 (and during the subsequent 1–3 annual intervals) might also be consistent with the relative body condition results we found for upper-reach Colorado pikeminnow during this period. Mean *Kn* in the upper reach was significantly lower in 1998 than it had been when fish were last sampled in 1994, and it remained low through at least 2000. We might speculate that net downstream movements during and after 1999, heretofore not observed during the prior eight years, might have been related to individuals seeking better feeding conditions than they were experiencing in the upper reach at that time. The subsequent reversal in direction of net movement in 2003 (no additional downstream movements) coincided with a significant improvement in mean *Kn*. Unfortunately, there were no data collected on forage fish relative abundance that might be used to help link downstream movements to temporary changes in upstream feeding opportunities. Alternatively, occasional net downstream movements may be largely random or driven by unknown environmental causes.

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). Using the recent 2004–2010 matrix, no time effect was detected. Hence, annual rates of transitions were calculated as identical for periods 2008–2009 and 2009–2010. In addition, upper-to-lower reach movements were so sparse in the recent period that the reduced matrix calculated unrealistic transition probabilities (100% for the last two annual periods) that were considered unreliable.

Electrofishing Catch-per-Effort

In the past, ISMP used annual electrofishing catch rates as a means to discern trends in Colorado pikeminnow population abundance. 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, Osmundson and White 2009), 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.

Despite the shortcomings of catch rates, they can provide something of a consistency check for trends indicated by annual abundance estimates. We superimposed mean annual electrofishing catch rates of Colorado pikeminnow over our 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 (Figure 4), 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 and 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. 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), 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 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 (see Results). These two sites were physically altered to reduce high selenium concentrations in the water and biota by flushing the sites with river water. This was accomplished by facilitating the flow of river water into the habitats from the upstream end by installing control structures or excavating coarse sediment. The former pond-like habitat extending up from the mouths of the channels was subsequently transformed into flowing side channels during spring runoff, thereby losing the zero-velocity, warm conditions that formerly attracted Colorado pikeminnow and allowed trammel netting. A gated-pipe control structure at WSWA was installed in winter 1996 and was initially operated infrequently; however, over time, entrained fine sediment from the flowing water filled in the former ponds. Later, in 2004, a large section of the upstream dike at WSWA was removed, creating a seasonal side channel that now routinely flows during spring runoff, with the control structure no longer being used. At Island Backwater, the seasonally dry upper end of the channel was excavated in 2003, allowing water to flow through at much lower main-channel discharges. Hence, beginning in 2003, the lower end of the channel ceased functioning as a backwater during spring runoff. 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.

Catch Rates of Sympatric Species

Based on the dissimilarities between Colorado pikeminnow abundance estimates and netting catch rates described above, trammel-net capture rates of other fish species that share backwater habitat with Colorado pikeminnow likely also reflect relative use of backwaters during runoff and not necessarily relative abundance in the river. Unfortunately, there currently is no separate long-term index of abundance with which we can compare trammel-net capture rates for sympatric species like there is for Colorado pikeminnow (i.e., no mark-recapture abundance estimates). Capture rates significantly declined over the 19-year study period for one native species, roundtail chub, and for two non-native species, common carp and channel catfish. In the past, trammel-net capture rates were assumed to reflect changes in population abundance (see Osmundson 2002). However, based on the discrepancies noted above for Colorado pikeminnow, we urge caution in drawing conclusions about trends in populations of sympatric species from the backwater trammel-net data alone. From a non-native fish management standpoint, downward trends in capture rates of common carp and channel catfish may be of some interest to native fish managers. Certainly, the decline in captures of the native roundtail chub, though perhaps not necessarily reflecting a general decline in the local population, should prompt development and initiation of additional and more conclusive monitoring techniques for this species.

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. Hence, 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 20-year, 1991–2010 period, two 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. Although high catch rates of YOY Colorado pikeminnow in fall seine surveys may portend strong year classes, 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. Hence, 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 two 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. The general trend over the recent 13 years, from 1998 to 2010, 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. Hence, 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 12 annual length-frequency distributions (and age-4 and age-6 in seven others) suggests there were only two strong year classes produced during the 20-year period of 1986–2005. These two years, along with six 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, our most recent length-frequency data suggests that after year 2000, there were four more 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 2010.

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. In our most recent year of study (2010), age-5 fish would have been of the 2005 year class. Not until 2013 sampling data are analyzed will we have length data with which to gauge the strength of year classes from 2006, 2007 and 2008.

Relative Abundance of YOY and Later Strength of Recruitment

A fish year-class is strong at age-5, or when later recruiting to the adult population, because young were produced in high numbers in the year of origin, or because survival during the juvenile phase was especially high, or perhaps for both reasons. An understanding of how environmental factors affect production of young and survival of juveniles (and ultimately recruitment level) is required before managers can hope to devise effective strategies aimed at increasing the size of this small population. As a first step, it would be useful to identify the stages when cohorts are most susceptible to negative environmental pressures. In theory, this can be done by tracking cohorts and identifying when significant declines in relative abundance occur. Identifying the occurrence of declines would aid in accomplishing the second step: identifying the primary environmental pressures that lead to mortality. Although these questions seem obvious, answers have remained elusive since researchers began studying Colorado pikeminnow populations over 30 years ago.

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. Part of the adaptation to such a variable environment is the expectation that there will occur years of high and years of low reproductive success and years of high and years of low juvenile survival. Over time, successful years will make up for unsuccessful ones. High egg output and long life are traits that aid population persistence when there occur 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. Young Colorado pikeminnow can be captured in backwater nursery habitat with beach seines during their first year of life. Standardized, young-of-the-year sampling in fall (late September-early October) provides an index of relative abundance at this early life stage. YOY 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. 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.

It makes intuitive sense that, in general, fish are most vulnerable to the vagaries of 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 CPE) 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 CPE 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.

Both Valdez and Cowdell (1999) and McAda and Ryel (1999) found significant correlation between CPE of YOY in fall with CPE the following spring. Though puzzling at first, given the high annual variation in survival, it makes sense that if CPE is low in fall it will also be low in spring and unless an abundant cohort has relatively low over-winter survival, CPE should still be high in spring relative to other year classes.[1] 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.

McAda and Ryel (1999), noting the high CPE in 1996 as well as the relatively high overwinter survival to spring 1997 (77%) suggested it would be interesting to see how well this cohort would later recruit to the adult population. They also suggested that later adult recruitment level of the 1994 year class would be interesting because, though low in abundance, individuals were of the largest size of all year classes studied. The fate of these two year classes (1996 and 1994) might therefore help determine whether abundance or size as YOY would later prove to be the best predictor of adult recruitment (McAda and Ryel 1999).

When we compared long-term data from annual YOY sampling with length frequencies of Colorado pikeminnow electro-fished and trammel netted five years later, we 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, despite it having high first-year, over-winter survival. 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. Of the 20 year classes for which we have both fall YOY CPE data and a qualitative assessment of strength at age-5, twelve displayed a consistency in relative abundance between age-0 and age-5. Of all possible combinations, the outcome with the highest probability (75%: 95% CI: 41-95%) was a weak year class at age-0 remaining weak until age-5. A strong year class at age-0 had only a 50% probability of remaining strong until age-5 (95% CI: 3.8–96.2%). This does, however, represent a higher probability than a weak year class later becoming strong (12.5%: 95% CI: 0.8–44.6%), thereby suggesting that a year class with high abundance of YOY in fall is more likely to later recruit in higher numbers than an initially weak year class.

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[1] In the Colorado River, only one of nine cohorts was abundant, and if overwinter survival had been low that year, there would have been no correlation between fall and spring CPE (McAda and Ryel 1999).

The two probabilities were not, however, significantly different. Although we conclude that catch rates of YOY in fall are of limited use in forecasting future strength of the same year-class when it approaches the adult stage, one point is clear: the high frequency of years with weak year classes at the YOY stage, beginning in 1997, will likely result in a high frequency of weak recruitment years. This does not augur well for this population.

Inconsistency in relative cohort strength between age-0 and age-5 in roughly 40% of the 20 cases 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 downstream 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 our 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 served as stable 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 the 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. We encourage researchers to explore these and other possible sources of annual variation in juvenile survival that occur after the first winter.

Body Condition and Population Abundance

We found a very weak, negative, non-significant relationship between body condition and abundance for adults in the upper reach. In the lower reach, there was a slightly stronger relationship that was almost statistically significant; however, the relationship was positive, suggesting that condition improved as adult Colorado pikeminnow abundance increased. Linear regression is not an altogether valid test for this because the independent variable (abundance estimates) should, in theory, be free of error; in this case, both the independent and the dependent variable have variance associated with them. This makes it more difficult to discern a relationship if indeed there is one.

In the upper reach, it is unlikely a relationship exists, at least not at currently low abundance levels, given the low r^2 (0.13) and high p (0.23) value. The lower reach results provide a non-intuitive situation with condition apparently improving with increased abundance. If real, one explanation might be that when forage becomes scarce, condition declines, prompting individuals to migrate to the upper reach, thereby reducing abundance in the lower reach. Conversely, when forage is plentiful, condition increases and more fish remain in the lower reach rather than migrating upstream, thereby resulting in both good body condition and increased abundance. When looked at in this way, condition becomes the independent variable that drives abundance of adults within the lower reach. Unlike in a lake or pond environment, where over-reproduction can lead to low condition or stunting in fish, the 'open' nature of rivers allows relief through emigration when resources temporarily become scarce. This explanation for the lower reach is plausible, but we are not concluding that a real relationship exists given the relatively low r^2 (0.28), non-significant p (0.08) value, and the fact that means and estimates (with associated variance) were regressed.

If food resources become scarce at times in the lower reach, it likely occurs at relatively low adult Colorado pikeminnow densities. Based on abundance point estimates, densities of Colorado pikeminnow $\geq$ 450 mm TL ranged from 1.4 to 4.4 fish/mile (0.85 to 2.7 fish/km) with a mean of 2.7 fish/mile (1.6 fish/km). The significant declines in body condition in the lower reach as Colorado pikeminnow grew from juvenile to adult sizes, coupled with the upstream dispersal of fish at this same life stage supports the possibility that upstream dispersal is prompted by limited feeding opportunites for adults in the lower reach.

In the upper reach, where no relationship between abundance and body condition was detected, food resources were probably not limiting at the adult densities observed during our study period. An exception to this may have been during 1998–2000; when mean body condition declined suggesting that feeding opportunities may have been temporarily reduced. Upper-reach density of Colorado pikeminnow $\geq$ 450 mm TL in 2005, the year with the highest abundance estimate, was 7.5 fish/mile (4.7 fish/km), assuming 477 adults over 63.5 miles. Osmundson et al. (2002) documented electrofishing catch rates of forage-size fish (100–300 mm TL) 4.5 times higher in the upper reach than in the lower reach during a 1994–1995 study. We would therefore expect the upper reach to be capable of supporting higher densities of adult-size Colorado pikeminnow than the lower reach. Once in the upper reach, body condition improved with increased length, suggesting improved feeding opportunities for adults. This might be explained by higher forage densities and because a wider array of forage sizes can be consumed as adults attain larger sizes. Using the mean density of 2.7 fish/mile as what the lower reach might generally support, along with the above comparison of forage abundance in the two reaches, 11.6 adults/mile (7.2 adults/km) can be derived as an estimate of adult densities the upper reach might support. Such extrapolations provide very rough approximations and assume much, but are useful in supporting the premise that population abundance in the upper reach is most likely limited by the infrequency of strong year classes rather than food resource limitations, at least at the low population densities observed there during the past 20 years.

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 two exceptions to closure worth noting here: one entailed between-reach movements, and the other, movements to and from the Green River system.

Of the 55 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. Also 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 documented over a 20-year period, only one was known to have occurred during an annual sampling period (Appendix Table VI). 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 21 marked fish that we know emigrated from our study area to the Green River over a 20-year period (about one 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 400–450 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 phase is needed.

Inter-System Movements

Conclusions regarding net 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 other 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.). For instance, the higher percentage of detected immigrants (1.15%) in the Colorado River system than in the Green River system (0.29%) may in part be explained by the much higher number of tagged individuals in the Green River system that could move and be detected in the Colorado system compared to the number tagged in the Colorado River system. Similar caution must be urged in interpreting emigration rates: the estimated proportion of Colorado-River-tagged fish that emigrated to the Green River system (2.7% compared to 1.0% of Green-River-tagged fish that emigrated to the Colorado River system) may be biased by the higher long-term recapture rate in the Colorado River system (40% in the Colorado River system; 29% in the Green River system). Hence, Green-River-tagged fish may have a higher chance of being detected in the Colorado River once they have moved there compared to detection of those Colorado River fish that moved to the Green River. So-derived statistics may thereby underestimate the real difference in percentages of those multi-captured fish that moved between systems. Clearly, of the two populations, a greater percentage of the Colorado River group is lost to the neighboring system. The more important question is whether these losses from the Colorado River population via emigration were balanced by immigration. Biases associated with unequal sampling regimes do not allow strong inferences to be drawn from the above numbers. However, based on the 21 fish that we know emigrated (and presumably did not return) and the 21 fish that we know immigrated (and presumably stayed), we can speculate that if there was a net movement out of the Colorado River system, it was probably relatively small.

Although the two systems are treated as separate populations for research and management purposes, 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), a summarization of which is provided here.

Colorado pikeminnow movement between the Colorado and Green river systems requires cautious interpretation. Although movement between the systems suggests gene flow between the populations, it does not provide direct evidence of it. Osmundson and White (2009) earlier described possible scenarios that would allow for gene flow as well as other scenarios where gene flow would not occur. Both outcomes are possible. The most definitive evidence of gene flow would be the capture of a given fish on the spawning grounds of one river system in one year and on spawning grounds within the other river system in another year. Or, perhaps an adult present in one river system during the estimated spawning season and then present in the other river in another year during the estimated spawning season. So far, neither scenario has been documented. However, although gene flow has not been verified, it seems likely that it is occurring. Even if these fish have fidelity to their natal river or spawning location when it comes time to spawn, as has been suggested (see Tyus 1985), it is likely that some percentage of each population ‘stray’ and spawn in a river other than their river or stream of origin, as is the case with salmon (Quinn et al. 1991). Those few sub-adult or adult fish that make substantial movements downstream in one river and upstream in the neighboring river may represent a small segment of the population that does not establish a strong fidelity to a home range and can be considered ‘wanderers’, perhaps foraging or spawning in more than one river during their lives. Even if the vast majority of fish of each population possesses a strong affinity for its natal river, such wanderers may provide a small but important level of gene flow between the populations. In addition, such wanderers may provide an important function over evolutionary time by re-colonizing rivers where populations have died out for one reason or another, such that the two rivers function as an abbreviated metapopulation.

As previously described by Osmundon and White (2009), the metapopulation concept seems to fit the groups of Colorado pikeminnow inhabiting the Green and Colorado river sub-basins because each has discreet breeding populations connected by migration, such that recolonization is possible (affecting long-term meta-population dynamics) but that the exchange rate of individuals is so low that migration has no real effect on local, short-term, population dynamics (Hanski and Simberloff 1997). The low rate of intersystem movements documented here supports the idea that short-term population dynamics are not affected by migration. Additionally, if migration between the systems was significant, the dynamics of the receiving population would show some correlation to those of the donor population. To date, this has not been the case: demographic dynamics of Colorado pikeminnow in the two systems appear to behave independently (see Osmundson and White 2009 for examples). In summary, even though there is probably enough errant movements into the adjoining river to keep the two groups from differentiating genetically over time, the two groups are demographically isolated enough that population dynamics function separately. Hence, a population suffering from low recruitment in one system will not be ‘rescued’ by migrants from the neighboring system.

A question germane to evaluating prospects for long-term persistence of these populations is whether one river might serve as a source for recolonization if the population in the neighboring river was extirpated. Because of its smaller size, the Colorado River population of Colorado pikeminnow is the more likely of the two populations to become extirpated through demographic stochasticity (random fluctuations in population abundance) at some time in the future. If the extirpation was caused by this we might assume recolonization from the Green River would occur over time as theorized by the metapopulation concept, i.e., if prolonged low recruitment occurs by chance, such that it does not keep pace with mortality for an extended period, the population could ‘wink out.’ Intersystem movements of Colorado pikeminnow from the neighboring Green River population, even at a low rate, could theoretically ‘restart’ a population in the Colorado River over time. However, if prolonged low recruitment does not occur by chance, but rather because environmental conditions have changed to the point where reproduction or survival of young becomes too depressed, the neighboring donor population cannot be expected to ‘restart’ the extirpated population until the environmental conditions conducive to reproduction and survival are restored. For managers, the worrisome aspect of this is our poor understanding of the factors critical to successful reproduction and survival of young. We cannot assume recolonization will occur in the event of extirpation if we do not possess the understanding of, nor means to restore, critical aspects of the habitat.

Fish Stockings and Fish Ladders

Colorado pikeminnow stocked in the Colorado River had low survival and/or retention (4%) during their first year at large. Based on the distribution of captures, it appeared that most, if not all, fish dispersed downstream after being stocked, with an unknown number entrained in Grand Valley irrigation canals. About half of those caught from the river were found downstream of Moab, Utah, suggesting that many of those that did not die may have moved out of our study area and perhaps into Lake Powell. The four that were caught in 2008 indicate some limited (0.3%) survival of this group in the river over the first 3-4 years. However, subsequent captures dropped to zero over the next two years. One of the primary objectives of stocking these fish was to speed recovery in the unpopulated reaches upstream of the diversion dams (Nesler 1998, Nesler et al. 2003). This objective was evidently not met. None of these Colorado pikeminnow has been found in the upstream reaches of the Colorado River where they were stocked despite extensive sampling there by electrofishing crews searching for smallmouth bass (B. Burdick, USFWS, personal communication). To date, no surviving stocked fish have attempted to return to their stocking reach based on fish trap monitoring at the Grand Valley Project Diversion Dam (GVPDD) on the Colorado River and the Redlands Diversion Dam (RDD) on the Gunnison

River. This might be explained by the extremely low survival or retention rate of the stocked fish in the Colorado River downstream of the diversion dams.

Although wild Colorado pikeminnow are occasionally captured ascending the Gunnison River at the RDD ladder (Burdick 2001, Francis and Ryden 2012a), few have apparently remained upstream of the dam. Between 1996 and 2013, 124 captures of Colorado pikeminnow were made at the RDD ladder trap, including 105 unique fish. Of these, 22 (21%) were subsequently captured either in the Gunnison River downstream of the ladder or in the Colorado River. Three were subsequently captured in the Gunnison River upstream of the ladder; however, two of these were later captured in the Colorado River downstream. During six electrofishing trips in recent years (two annual trips in 2011, 2012 and 2013) from Delta to Redlands Diversion Dam only one Colorado pikeminnow was captured in the Gunnison River (October 2012), and it was a fish that had recently come through the ladder (USFWS unpublished data) .

Upstream movements past the diversion dams on the Colorado River have also not met expectations (e.g. Valdez and Muth 2005). During 2009 and 2010, one wild Colorado pikeminnow was captured in the reach between the Price Stubb fish ladder and the GVPDD. Additionally, a remote PIT-tag antennae detected the movement of ten different individuals past the Price Stubb fish ladder during 2010–2012, demonstrating use of the relatively new ladder (Francis and Ryden 2012b). However, no Colorado pikeminnow have yet been found in the fish trap at the more upstream GVPDD fish ladder since operation began in 2005 (Francis and Ryden 2013). 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, both stocking and fish passage have largely failed to populate upstream reaches. Prospects for recovery of the Colorado River population would be enhanced if the river’s major tributary, the Gunnsion River, could be repopulated. An extension of range into a tributary would insure 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. 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.

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 2010, 493.

-- The minimum AIC_c model for the new 2004–2010 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 (2003–2010). During the most recent study period (2008–2010), capture probability in the lower reach was generally higher than and significantly differed from that in the upper reach.

-- 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 72.7% (2008–2010), although additional monitoring will be needed to confirm this trend.

-- Precision of annual abundance estimates was generally higher in the upper reach than in the lower reach. Nine of 12 coefficients of variation (CV) for the summed-reach estimates were < 20%. During the most recent sampling period (2008–2010) the mean CV was 13.2%, the best of the four multi-year efforts.

-- During the 20-year study period, the population remained self-sustaining. This was evidenced by: 1) 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, and 2) results of a weighted regression analysis of river-wide adult abundance estimates that indicated the intercept-only model as having the greatest weight, suggesting population stability. However, weighted regression of just the upper-reach adult population gave greatest weight to the quadratic model, suggesting the population increased and then later declined.

-- Trends in electrofishing catch rates generally tracked the trend in abundance point estimates when the two indices were compared for years 2003–2010, a period when sampling gear and protocols remained consistent. The closest agreement was for fish ≥ 450 mm TL. Both indices indicated an increase in abundance that peaked in 2005 and then declined. Trammel net catch rates, however, did not match trends in abundance estimates. In the lower reach, there was an overall decline in trammel-net catch rates. In the upper reach, catch rates peaked in 1998 and then declined.

-- Trammel net catch rates of sympatric species inhabiting backwaters during spring runoff significantly declined for roundtail chub, common carp, and channel catfish.

-- 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 young-of-the-year may not be reliable predictors of later recruitment levels. 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.

-- We found no correlation between abundance and mean body condition of adult Colorado pikeminnow. Food availability does not appear to limit upper-reach adult abundance at population levels observed in the past 20 years.

-- Some Colorado pikeminnow moved between the Colorado River and Green River systems. Fifty-four inter-system movements between 1990 and 2010 were documented from capture-recapture records obtained from the Recovery Program's PIT tag database, representing 1.61% of the 2,976 unique Colorado pikeminnow that were captured two or more times. Net movements in each direction appear relatively balanced and occur at a low enough frequency that the demographics of one system have a negligible effect on the demographics of the neighboring system.

-- Juvenile Colorado pikeminnow (100–350 mm TL) stocked into reaches upstream of the study area in both the Colorado and Gunnison rivers in 2003 and 2004 either died or dispersed downstream into the study area and probably beyond. An estimated 3.7% of the total number stocked (5,084) were present in the study area in 2005. By 2008, an estimated 0.3% of those stocked remained. In 2009, one was captured; in 2010, none.

-- Some dispersal through the new Price-Stubb fish ladder has occurred, but none past the more upstream Grand Valley Project Diversion Dam on the mainstem Colorado River. Based on the downstream dispersal of stocked fish and the non-retention of upstream migrants, suitability of habitat upstream of the diversions may limit upstream expansion of the population in both rivers.

-- 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. However, very low abundance in the past and recent declines in abundance over a short time period do not instill confidence that long-term persistence is assured. 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.

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. A reasonable goal is to conduct four sampling passes per year. It does not appear possible to fit five complete passes in prior to the Colorado pikeminnow spawning period. Also, increasing current levels of effort per pass is probably not practical.

3) We recommend that any hatchery-reared Colorado pikeminnow be marked with PIT tags before being stocked in the upper Colorado or Gunnison rivers. It is essential that stocked fish can be reliably identified as such when they move downstream and mix with wild pikeminnow. Stocking will likely be unsuccessful in repopulating upstream reaches until wild Colorado pikeminnow demonstrate suitability of habitat by colonizing these areas of their own accord.
4) We recommend initiating an annual larval monitoring program in the Colorado River using drift net sampling as has been done in the Green River system. Developing techniques to track cohorts from age-0 to age-5 is needed to identify survival bottlenecks during the juvenile phase and ultimately determinates of recruitment strength. Understanding factors affecting reproductive success (as measured by larval production) is the first step in this process.
5) 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. Effective management actions cannot be developed toward this end without understanding factors that affect recruitment strength.

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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 length at Age 2 are from small fish captured in June 2013 from the lower reach and assumed to be two years old. Mean lengths of Ages 3–7 are from measurements of fish aged using scales. 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 updated from those provided in Osmundson et al. (1997).

Age		Total length (mm)			Growth period	Annual growth increment (mm)	
(years)	*N*	Mean	Range	SD	(age)	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	71.4	
2	57	147.9	114-183	12.8	2–3	90.1	
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, 1991–2010. Probabilities are presented for secondary (passes) and primary (year or 'all') capture occasions. For years 1991–2005, probabilities are standardized for fish = 500 mm TL because the top model indicated a length effect (probability varied by fish depending on length); for years 2008–2010, probabilities are for any fish because the top model indicated no length effect.

	Length	Upper Reach passes						Lower Reach passes					
Year	(mm)	1	2	3	4	5	all	1	2	3	4	5	all
1991	=500	0.087	0.067	0.099	--	--	0.233	--	--	--	--	--	
1992	=500	0.061	0.070	0.067	--	--	0.185	0.045	0.037	--	--	--	0.080
1993	=500	0.104	0.108	0.115	--	--	0.293	0.091	0.073	--	--	--	0.157
1994	=500	0.066	0.088	0.090	--	--	0.225	0.104	0.049	--	--	--	0.148
1998	=500	0.091	0.143	0.107	--	--	0.304	0.087	0.170	--	--	--	0.242
1999	=500	0.105	0.132	0.109	--	--	0.308	0.100	0.065	--	--	--	0.159
2000	=500	0.105	0.107	0.057	--	--	0.246	0.068	0.039	--	--	--	0.104
2003	=500	0.027	0.037	0.039	0.027	--	0.124	0.011	0.017	0.043	0.041	--	0.108
2004	=500	0.047	0.040	0.119	--	--	0.194	0.043	0.055	0.043	--	--	0.135
2005	=500	0.037	0.050	0.043	0.077	0.064	0.244	0.049	0.094	0.089	0.068	0.066	0.317
2008	N/A	0.042	0.037	0.042	0.050	0.040	0.194	0.039	0.087	0.106	0.069	--	0.270
2009	N/A	0.037	0.048	0.118	0.055	0.085	0.301	0.033	0.102	0.089	0.062	--	0.258
2010	N/A	0.051	0.069	0.055	0.080	0.062	0.279	0.064	0.047	0.108	0.131	--	0.309
Mean		**0.066**	**0.077**	**0.082**			**0.241**	**0.061**	**0.070**				**0.191**
SE		0.008	0.010	0.009			0.016	0.008	0.012				0.024

Appendix Table III. Abundance estimates ($\hat{N}$) for Colorado pikeminnow ≥ 250 mm TL in the lower and upper Colorado River study reaches, and for the reaches combined, with lower and upper bounds of 95% confidence intervals (CI) and standard errors (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	535.8	408.4	730.2	80.6	166	15.0
2008	335.3	236.2	501.0	65.8	89	19.6
2009	310.7	219.4	461.8	60.3	80	19.4
2010	298.5	217.0	433.1	53.7	92	18.0
			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	483.8	376.1	640.6	66.5	140	13.7
2008	408.5	282.4	613.3	82.4	80	20.2
2009	273.6	205.9	378.3	43.2	82	15.8
2010	288.1	212.7	406.4	48.4	80	16.8
			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	1,019.7	852.9	1,237.3	97.4	306	9.5
2008	743.8	572.7	987.4	104.5	169	14.0
2009	584.3	461.2	758.0	74.8	162	12.8
2010	586.6	466.3	756.1	73.1	172	12.5

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 bounds of 95% confidence intervals (CI) and standard errors (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	412.1	313.1	565.8	63.2	134	15.3
2008	302.1	217.4	439.1	55.3	80	18.3
2009	237.0	165.3	358.0	47.8	61	20.2
2010	204.5	145.7	305.1	39.5	63	19.3
			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	477.1	371.5	630.6	65.2	138	13.7
2008	407.8	285.6	602.5	79.1	80	19.4
2009	273.8	205.7	379.3	43.4	82	15.9
2010	288.3	212.0	408.6	49.1	80	17.0
			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	889.2	746.2	1,075.4	83.4	272	9.4
2008	709.9	544.9	945.5	100.9	160	14.2
2009	510.9	403.7	662.0	65.1	143	12.7
2010	492.8	389.8	638.7	62.7	143	12.7

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 bounds of 95% confidence intervals (CI) and standard errors (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	257.2	188.3	372.9	45.8	87	17.8
2008	253.6	176.7	384.3	51.5	67	20.3
2009	209.8	145.4	319.4	43.1	54	20.6
2010	197.9	141.6	293.6	37.7	61	19.1
			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	398.5	309.8	528.3	54.9	118	13.8
2008	407.2	281.6	611.1	82.1	80	20.2
2009	267.3	200.8	370.2	42.4	80	15.9
2010	288.3	212.8	406.8	48.5	80	16.8
			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	655.7	540.3	810.9	68.4	205	10.4
2008	660.8	504.1	886.0	96.1	147	14.5
2009	477.0	376.5	619.1	61.1	134	12.8
2010	486.3	384.4	630.7	62.1	141	12.8

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 bounds of 95% confidence intervals (CI) and standard errors (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	23.2	7.5	202.1	33.0	6	142.0
2008	18.6	9.8	43.9	7.8	5	42.0
2009	7.8	3.4	26.5	4.9	2	63.2
2010	6.5	3.0	22.0	4.0	2	61.2
			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	23.1	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	1.6	1.0	134.9	27.3	1	1,726.8
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
			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	24.8	7.8	401.4	59.5	7	239.8
2008	18.6	9.8	43.9	7.8	5	42.0
2009	7.8	3.4	26.5	4.9	2	63.2
2010	6.5	3.0	22.0	4.0	2	61.2

Appendix Table VII. Documented movements of Colorado pikeminnow (captures and recaptures of PIT-tagged individuals) between rivers of the Colorado River sub-basin (mainstem Colorado and Gunnison rivers) and rivers of the Green River sub-basin (Green, White, Yampa, and Duschene), 1991–2010.

River 1[1]	**Rmi 1**[2]	**Date 1**[3]	**TL 1**[4]	**River 2**[5]	**Rmi 2**[6]	**Date 2**[7]	**TL 2**[8]	**Total miles**[9]	**Total Years**[10]
Colorado	58.3	1991 05-23	381	Yampa	73.0	1999 05-11	652	476	8
Colorado	54.1	1993 04-09	500	Green	160.0	1997 07-18	576	214	4
Colorado	21.7	1993 05-21	490	Yampa	94.8	1996 05-15	602	461	3
Colorado	90.2	1994 06-22	358	Green	254.8	2000 05–31	526	345	6
Colorado	62.0	1995 05-05	550	Green	112.5	2002 05-06	696	174.5	7
Colorado	53.3	1997 05-12	615	Green	184.6	1998 07-15	619	238	1
Colorado	133.4	1998 05-08	752	Green	90.1	2000 05-18	800	224	2
Colorado	26.5	1998 05-12	421	Duschene	2.0	1999 06-10	466	277	1
Colorado	58.2	1998 05-28	420	Green	269.9	2002 06-07	620	328.1	4
Colorado	43.8	1998 06-01	369	Green	182.2	2001 04-19	501	226	3
Colorado	67.7	1999 05-06	454	Yampa	41.6	2000 06-19	490	454	1
Colorado	26.5	1999 05-26	347	Green	89.0	2001 05-22	490	115.5	2
Colorado	16.5	1999 05-27	450	Green	52.2	2002 04-25	545	68.7	3
Colorado	43.9	1999 06-08	429	White	101.5	2001 04-16	480	391.6	2
Colorado	58.2	2000 05-10	470	Green	50.0	2002 05-12	562	108.2	2
Colorado	15.2	2003 05/30	688	Green	17.4	2006 06/21	785	32.6	3
Colorado	58.3	2003 05/27	415	Yampa	59.1	2007 05/02	570	462	4
Colorado	2.7	2004 05/20	404	Green	133.6	2007 04/07	500	136.3	3
Colorado	32.0	2005 05/24	498	Green	26.2	2006 05/30	558	58.2	1
Colorado	22.8	2005 05/11	504	Green	76.0	2006 05/27	540	98.8	1

Appendix Table VII (continued).

River 1[1]	**Rmi 1**[2]	**Date 1**[3]	**TL 1**[4]	**River 2**[5]	**Rmi 2**[6]	**Date 2**[7]	**TL 2**[8]	**Total miles**[9]	**Total Years**[10]
Colorado	32.2	2005 06/09	415	Green	35.0	2007 05/29	530	67.2	2
Colorado[a]	167.9	2000 03-09	557	Green	30.7	2001 05-28	570	198.6	1
Green[a]	30.7	2001 05-28	570	Colorado	168.2	2003 05-07	592	198.9	2
Gunnison[b]	25.3	2000 08-03	531	Green	261.8	2001 05-23	550	457.1	1
Green[b]	261.8	2001 05-23	550	Colorado	168.2	2003 05-07	589	430.0	2
Colorado[c]	58.2	2005 05/05	480	Green	21.4	2007 06/12	500	79.6	2
Green[c]	21.4	2007 06/12	500	Colorado	16.5	2008 05/21	517	37.9	1
Colorado[d]	98.8	2005 05/02	612	Green	71.8	2006 05/27	640	170.6	1
Green[d]	71.8	2006 05/27	640	Colorado	100.2	2009 05/29	708	172.0	3
Colorado[e]	22.0	2005 04/15	450	Green	97.0	2007 05/10	517	119.0	2
Green[e]	97.0	2007 05/10	517	Colorado	30.0	2010 05/18	566	127.0	3
Green	51.5	1991 05-08	330	Colorado	183.3	2000 05-01	587	235	9
Green	254.0	1995 05-10	519	Colorado	174.4	1999 06-16	597	428	4
Green	174.0	1995 07-27	445	Colorado	98.7	2000 05-05	585	273	5
Green	261.8	1996 05-01	576	Colorado	56.7	2004 05-26	720	318.5	8
Green	255.8	1996 06-10	567	Colorado	34.8	2000 05-15	596	291	4
Green	279.5	1998 04-15	625	Colorado	151.2	2003 07–31	643	430.7	5
Green	114.9	1998 05-05	540	Colorado	26.5	1999 05-26	542	141	1
Green	41.0	1999 05-12	462	Colorado	10.9	2003 04-10	611	51.9	4
Green	252.8	2000 04-26	612	Colorado	26.5	2000 05–31	617	279.3	0.1
Green	283.9	2000 05/04	505	Colorado	58.3	2005 04/20	548	342.2	5
Green	80.4	2001 05-23	721	Colorado	67.0	2004 04-14	773	147.4	3

Appendix Table VII (continued).

River 1[1]	Rmi 1[2]	Date 1[3]	TL 1[4]	River 2[5]	Rmi 2[6]	Date 2[7]	TL 2[8]	Total miles[9]	Total Years[10]
Green	12.0	2002 04-17	301	Colorado	51.3	2003 06-05	427	63.3	1
Green	103.7	2003 04-23	565	Colorado	175.5	2005 04-21	606	279.2	2
Green	229.8	2005 08/23	441	Colorado	16.5	2008 05/21	523	16.5	3
Green	46.0	2006 05/29	632	Colorado	79.5	2008 04/16	652	125.5	2
Green	8.0	2006 05/31	560	Colorado	16.5	2009 05/06	595	24.5	3
Green	26.0	2006 05/30	515	Colorado	141.5	2008 05/07	589	167.5	2
Green	62.0	2008 05/10	430	Gunnison	3.0	2010 07/29	569	235.0	2
Green	18.7	2008 05/12	532	Colorado	14.2	2009 04/22	546	32.9	1
Green	1.5	2008 04/30	545	Colorado	22.0	2010 05/19	594	23.5	2
Green	275.0	2009 06/04	506	Gunnison	3.0	2010 07/22	522	448.0	1
Green[f]	52.5	1994 05-10	458	Gunnison	3.0	1996 08-15	579	226	2
Gunnison[f]	3.0	1996 08-15	579	Green	0.5	2001 03-21	694	173.5	5

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[1] River 1 – river fish was last captured in prior to moving to River 2
[2] Rmi 1 – river mile location (measured from mouth of respective river) of last capture in River 1
[3] Date 1 – date of last capture in River 1
[4] TL 1 – length (mm) of fish at last capture in River 1
[5] River 2 – river fish moved to after last capture in River 1
[6] Rmi 2 –- river mile location (measured from mouth of respective river) of first capture in River 2
[7] Date 2 – date of first capture in River 2
[8] TL 2 – length (mm) of fish at first capture in River 2
[9] Total miles – distance traveled between last capture in River 1 and first capture in River 2
[10] Total years – years (approximate) between last capture in River 1 and first capture in River 2
[a] Fish-a that made two separate inter-river movements
[b] Fish-b that made two separate inter-river movements
[c] Fish-c that made two separate inter-river movements
[d] Fish-d that made two separate inter-river movements
[e] Fish-e that made two separate inter-river movements
[f] Fish-f that made two separate inter-river movements

Cover Photos:

Top: The Colorado River near Dewey (RM 91); looking downstream towards Fischer Towers and the La Sal Mountains, Utah, 2006. Photo by D. B. Osmundson

Bottom: Adult Colorado pikeminnow *Ptychocheilus lucius*. Photo by D. B. Osmundson

Colorado River Fishery Project
445 West Gunnison Ave., Suite 140
Grand Junction, CO 81501
970-628-7212
doug_osmundson@fws.gov

U.S. Fish and Wildlife Service
http://www.fws.gov

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