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Population Status and Trends of Colorado Pikeminnow of the Upper Colorado River, 1991-2005

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Final Report

July 2009

Prepared by

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EXECUTIVE SUMMARY

Mark-recapture studies from 1991 through 2005 were used to assess population trends of Colorado pikeminnow *Ptychocheilus lucius* in the upper Colorado River. Three multi-year data collection efforts were made: 1991–1994, 1998–2000, and 2003–2005. Primary objectives included capturing and marking Colorado pikeminnow ≥ 250 mm long from throughout the study area, developing estimates of population abundance and survival rate and assessing trends in recruitment. Although results of the first two study periods have been provided in previous reports, data from these earlier efforts were reanalyzed using new techniques. Here, a synthesis is provided of the updated information from the earlier studies and the results from the most recent study period.

The 287-km-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 Price Stubb Diversion Dam at Palisade, Colorado. The upper reach also included the lowermost 3.5 km of the Gunnison River downstream of the Redlands Diversion Dam at Grand Junction, Colorado. The 20-km Westwater Canyon, separating the 106-km upper reach from the 181-km 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 sampling effort, 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 were made through both reaches each year. In all three sampling periods, captured Colorado pikeminnow were measured, weighed, PIT-tagged and released.

The Huggins estimator within the robust design multi-state data type of Program MARK was used to generate abundance and survival estimates from mark-recapture data.

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.

Nine combined-reach annual abundance estimates and one earlier upper-reach estimate indicated the Colorado River population increased substantially in number during the study period. Point estimates of individuals $\geq$ 450 mm long in the most recent year, 2005, were 412 in the lower reach (2.3 fish/km) and 477 in the upper reach (4.5 fish/km), for a river-wide total of 889. Although no abundance estimate was available for the lower reach in 1991, the length frequency histogram of fish captured there that year suggested there were very few fish $\geq$ 450 mm TL present; hence the river-wide number of fish this size may not have been much greater than the estimate provided for the upper reach alone (i.e., around 200 individuals). Given that the 2005, river-wide, abundance estimate of fish $\geq$ 450 mm TL was over 800, the sub-population of fish this size might have quadrupled since 1991. Summed reach-specific abundance estimates generated with the Huggins model were about 14% higher on average than the summed estimates generated with Model M_o (upper reach) and M_t (lower reach) from program CAPTURE. Probability of capture varied among years and was generally lowest during the most recent three-year period despite the additional effort expended. Capture probability also varied by reach and fish length: for any given length, lower-reach fish had higher capture probabilities than upper-reach fish, and in both reaches, fish approximately 750 mm in length had capture probabilities 3–4 times that of fish 250 mm TL. Survival also varied by reach and fish length: fish in the upper reach had significantly higher survival rates than fish in the lower reach, and survival was maximized at fish lengths of 450–650 mm. Rates for smaller fish were not substantially lower. However, mortality rate was notably higher for very large fish (> 850 mm TL). Overall annual survival rates (combined-reach estimates) for fish $\geq$ 500 mm TL appeared to decline over time from 88% (1991–1994) to 86% (1998–2000) to 80% (2003–2005), but differences were not statistically significant.

Annual recruitment (number of fish 400–449 mm TL) appeared to exceed the estimated number of annual mortalities of fish $\geq$ 450 mm TL in six of the nine years for

which estimates were available. When annual gains and losses were summed there was an estimated net gain of 332 fish ≥ 450 mm TL. Lapses in sampling between the three multi-year efforts precluded estimating the total net gain for the period 1992–2005.

Precision of abundance estimates as measured by the coefficient of variation (CV) was lowest during the first multi-year effort (mean CV of 24%) and higher during the second and third multi-year efforts (mean CVs of 14% and 15%, respectively). Precision of estimates affects the ability to detect change in population abundance over time. Assuming precision of future efforts is similar to our most recent effort, the population would have to decline by 30% (between any two years used for comparison) for the difference to be statistically significant at $\alpha = 0.05$, and 24% at $\alpha = 0.10$.

Electrofishing catch rates (mean number of Colorado pikeminnow captured per hour), used in the past (Interagency Standardized Monitoring Program) as a means to detect trends in population abundance and as a consistency check for mark-recapture estimates, were found to not track trends in mark-recapture abundance estimates. A line fitted through the mean annual catch rates from 1986 to 2005 indicated no upward or downward trend. Although there was a substantial rise in catch rates from the late 1980s through the 1990s, recent catch rates were low again. This result probably stems from the generally low probability of capture experienced during the recent multi-year sampling period, but may also be related to differences in sampling protocol between the two studies and perhaps to changes in electrofishing gear. When the recent low capture rates were excluded, an upward trend was indicated by the ISMP catch rate results, consistent with that indicated by the annual abundance estimates.

Length-frequency histograms revealed a very strong year class (1996) of age-0 Colorado pikeminnow, previously documented from fall seine surveys, virtually disappeared before becoming large enough to be susceptible to electrofishing or trammel net sampling. Additionally, 1998 year-class individuals, scarce during fall seine surveys, later recruited to the adult population in relatively high numbers making it one of the strongest year-classes to recruit on record. These observations cast doubt on earlier conclusions that year-class strength in the year of origin is a good predictor of later recruitment strength. Our interpretation of the annual length-frequency histograms from both reaches was that in the 14 years from 1985 to 2000 there were seven very weak year-classes (based on relative

abundance of age-5 fish, 326-453 mm long) and only two very strong ones. However, the resulting recruitment rate was evidently an improvement over prior periods because adult abundance was very low at the start of our study.

Previous suggestions that the population had reached carrying capacity (based on a significant decline in relative body condition between 1994 and 1998) were not borne out by more recent results. The capacity of the system to support Colorado pikeminnow in good condition may have only been temporarily lowered. After the period 1998-2000 relative condition returned to levels similar to or higher than those observed in the first multi-year period. We found no relation between annual abundance and mean body condition of fish 500-599 mm TL; additionally, mean body condition in 1992 and 2005 was essentially the same even though abundance had significantly increased. Hence, if one uses a significant decline in body condition accompanying a significant increase in abundance as a signal that carrying capacity has been reached, we would have to conclude that this has not yet occurred.

The Recovery Program's database of PIT-tagged Colorado pikeminnow captured from throughout the Colorado and Green river sub-basins revealed that 29 individuals, or 1.4% of the total number of fish recaptured at least once, moved between the Colorado River and Green River systems between 1990 and 2005. This level of movement suggests enough gene flow to keep the two populations from differentiating genetically over time but not enough exchange of individuals for one population to affect the demographics of the other population.

Efforts to speed re-establishment of Colorado pikeminnow in reaches upstream of the diversion dams on the Colorado and Gunnison rivers through fish stocking in 2003 and 2004 were evidently unsuccessful. A high rate of long-distance downstream dispersal was documented during our study while other studies failed to recover any of the hatchery-raised fish in the reaches in which they were stocked.

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. Bestgen et al. (2007) recently provided abundance estimates from the first mark-recapture-based study (2000–2003) of the Green River population. Their point estimates ranged from 2,142 to 3,304 adults, depending on year. 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 recently augmented with hatchery-produced individuals (Ryden 2003). The mainstem Colorado River upstream of Lake Powell and upstream of the Green River confluence (Figure 1) hosts the second largest extant population. The status of this 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; annual abundance estimates from this work were presented 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). A third multi-year, mark-recapture field effort was conducted during 2003–2005. This report presents these recent results and provides a synthesis of results for the entire 1991–2005 period.

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 kilometers (rk) from the Green River confluence and were converted from river miles mapped by Belknap and Belknap (1974) and the Colorado Division of Wildlife (CDOW). The study area extended from the Green River confluence (rk 0.0) upstream to the limit of the fish's range at Palisade, Colorado, where the Price Stubb Dam (rk 303) blocked further upstream fish movement. For this study, the study area was partitioned into two major reaches, lower (rk 0–181) and upper (rk 201–303). The 20-rk-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).

The upper reach also included the lowermost 3.5 km 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, any Colorado pikeminnow tagged during our study that later moved upstream of the fish ladder were accounted for. Upstream movements through the ladder occurred primarily in July or August (one in early-September), either after the annual mark-recapture sampling was completed or during the last sampling effort of the year. Hence, this emigration from the study area did not violate the assumption of geographic closure for the within-year population estimates. Some of the individuals that used the ladder were later found using it a second or third time or were recaptured downstream of the dam in the lower Gunnison River or in the Colorado River, indicating they had passed down over the dam sometime after they first ascended it (Burdick 2001). 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

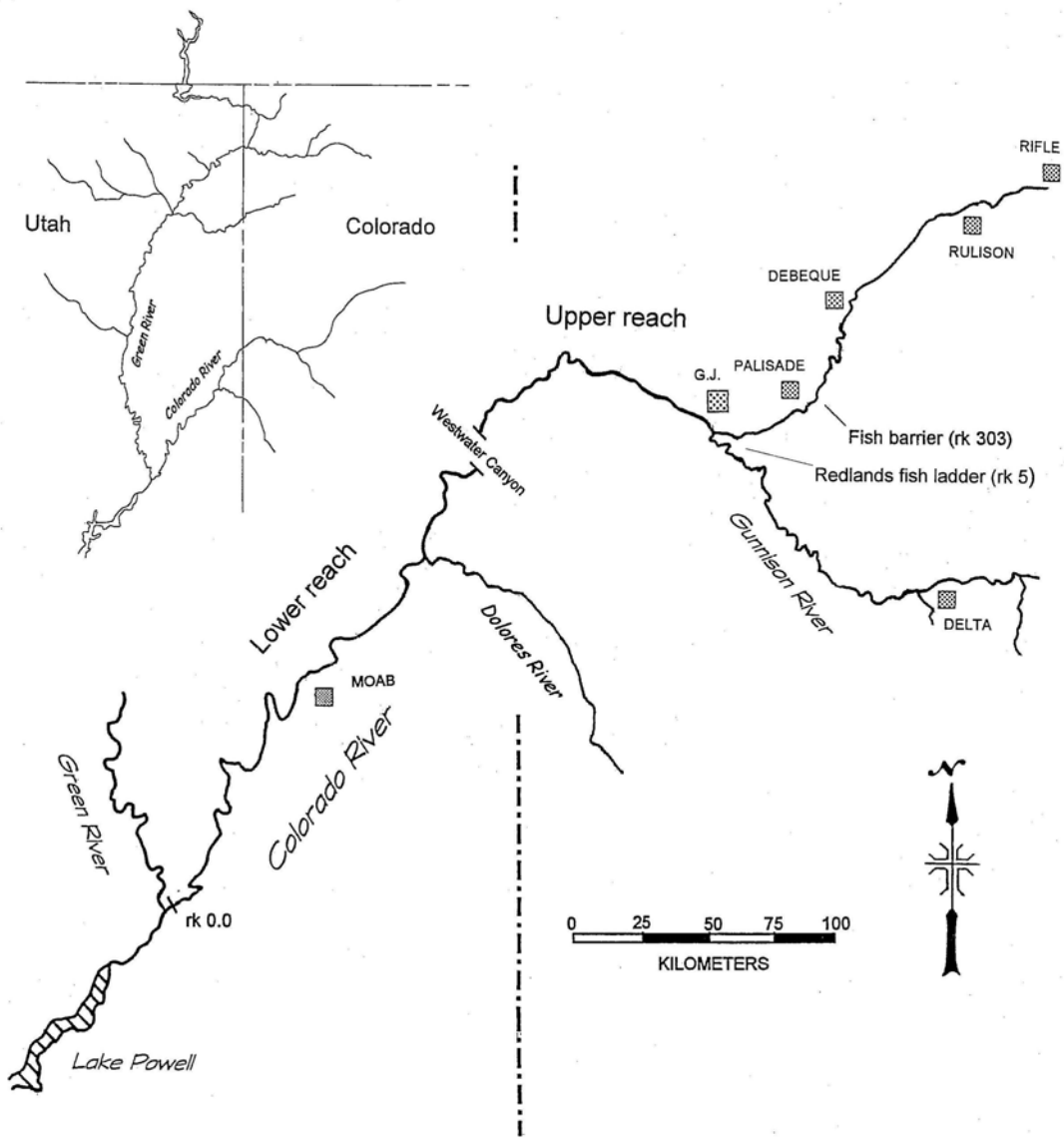

Figure 1. Map of the upper and lower reaches of the Colorado River study area. Downstream boundary of lower reach is river kilometer (rk) 0.0 and upstream boundary is the lower end of Westwater Canyon. Downstream boundary of upper reach is the upper end of Westwater Canyon and upstream ends are the fish barrier at rk 303 on the Colorado River and the Redlands fish ladder (rk 5) on the Gunnison River. Grand Junction is abbreviated G.J.

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. On the Colorado River mainstem, upstream dispersal remained blocked at the Price Stubb Dam (rk 303) during all three study periods.

Fish Capture and Marking

Capture methods during the 2003–2005 effort essentially followed those of the earlier two multi-year efforts, previously described in the aforementioned reports. Those procedures common to all three multi-year efforts are again briefly described here followed by a description of sampling variations unique to the recent 2003–2005 effort.

A combination of trammel-netting and electrofishing was used to capture Colorado pikeminnow ≥ 250 mm long during mid-April to mid-June. Trammel nets (1.8 m deep with a 2.5-cm-bar mesh inner panel and a 25-cm-bar-mesh outer wall) 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). Electrofishing was used to capture 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 johnboat 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. As soon as the last net was set, those set first were checked for fish. 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. 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 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. During 2003–2005, the number of passes varied by year (described below) and sampling began in early April prior to runoff so there would be sufficient time for additional passes. 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; and a Smith-Root GPP on some boats during the 2003–2005 effort. Both units produced pulsed DC.

During the two earlier multi-year efforts, capture data for portions of some passes were supplemented with capture records obtained from unrelated studies conducted by the CDOW, U.S. Fish and Wildlife Service (USFWS), and the Utah Division of Wildlife Resources (UDWR). During 2003–2005, capture records were supplemented 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 high during the first two multi-year efforts, one objective for the 2003–2005 effort was to capture and recapture more fish per year to reduce variance. The goal was to increase the number of passes per year and increase sampling effort per pass. Also, the unequal number of passes in the two reaches (three in the upper; two in the lower) during the first two multi-year efforts meant that length frequencies had to be calculated for each reach separately (more effort in one reach would result in over representation of sizes specific to that reach). Therefore, an additional goal for the 2003–2005 effort was to have an equal number of passes in the two reaches so that one length-frequency could be developed each year that would reflect the whole-river population.

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 2005, increased runoff 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.

The number of passes made through the study area varied annually. In 2003, four sampling passes were made through both the upper and lower reaches. In 2004, a rapid decline in water levels in June resulted in an early initiation of Colorado pikeminnow spawning activities and 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 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, data were assembled from Colorado pikeminnow captures made in July during the non-native fish removal project.

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; columns represented 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.

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. To do so, three models were fitted to the measured lengths: von Bertalanffy, logistic, and Richards (1959). For fish that were captured more than once within a year, the mean of the measured lengths was used for that year. The von Bertalanffy model provided the best fit of the three models based on the smallest mean squared error, so it was used to interpolate/extrapolate missing lengths. To fit each of the three models, a difference equation was assumed, following generally the procedures of White and Brisbin (1980). For the von Bertalanffy model:

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

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 passes. Data on two fish, captured in both the lower and upper reaches within the same year, had to be changed to be compatible with this model, which assumes no transitions (movements between reaches) within a primary occasion. In both cases, the fish were captured first in the lower reach, so the second capture (in the upper reach) was changed to a lower-reach capture.

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 included year, reach and fish length. Transition probabilities from lower to upper reach

(ψ^{LU}) and upper to lower reach (ψ^{UL}) were computed for intervals between primary occasions as a function of year, reach, and fish length.

Population 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. The Huggins estimator was used because the individual covariate length was a predictor of capture probability. To model the temporal variation in p within and between primary occasions, we also considered models of p that included flow, water temperature, and number of boat days for each pass. Flow was the mean discharge (cfs) of the days during which sampling took place, as measured at the USGS gauge at the Utah-Colorado state line. Because sampling days for each pass were not always synchronized between reaches, mean discharge was calculated separately for each reach. Mean temperatures were calculated the same way. Because trammel-netting and electrofishing were not comparable in terms of effort, we used boat days as a measure of effort, albeit a rather coarse one.

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 into the confidence interval. 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. However, no

summed estimate is provided for the first year, 1991, because no lower-reach estimate was available for that year (only one sampling pass was made). 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 during the study period 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). We also used the variance components module of MARK to fit a trend line to the estimates, a technique that takes the variance around the point estimates into account. In addition, shrinkage estimation was used to produce a set of shrunk estimates, estimates that have the sampling variance of the maximum likelihood estimates removed to produce estimates closer to the trend line. A Wald chi-square statistic was then used to test for a slope different than zero.

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).

Recovery Goal criteria also require that for downlisting to occur, populations must not significantly decline during the five-year monitoring period (USFWS 2002). The monitoring period is set to begin the year in which the Green River and Colorado River populations equal or exceed the adult population size targets. A simple method of evaluating decline is to compute a *z*-statistic from two estimates ($\hat{N}_1$ and $\hat{N}_2$) and their associated standard errors [$\mathrm{SE}(\hat{N}_1)$ and $\mathrm{SE}(\hat{N}_2)$]:

$$z = \frac{\hat{N}_1 - \hat{N}_2}{\sqrt{\mathrm{SE}(\hat{N}_1) + \mathrm{SE}(\hat{N}_2)}}.$$

Although the CV will vary from year to year, some idea of the magnitude of the decline required for it to be significant can be obtained by computing the z-test with various artificial point estimates and associated CV levels and then observe how the *P* values vary. For simplicity and illustrative purposes, the CV used was the same for both abundance estimates, and the SE of each estimate was determined by $\hat{N}$ and the CV. Using CVs typical of those encountered during the study period we calculated the percent decline required for the decline to be significant at α = 0.05 and α = 0.10. For these exercises we set $\hat{N}_1$ to 1,000 individuals and $\hat{N}_2$ to various values less than a 1000.

Electrofishing 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 (this study) were computed to extend the long-term catch rate results and to see whether ISMP sampling reaches provided a good representation of river-wide catch rates. Means were calculated for each pass by reach and for the entire study area (reaches combined), and for all passes combined by reach and for the entire study area. Separate means were also calculated for just those sub-reaches regularly sampled during ISMP (see McAda 2002). Calculations of catch rates for 2003–2005 included all Colorado pikeminnow large enough to be PIT tagged (≥ 200 mm TL). However, calculations of mean catch rates used for comparison with earlier ISMP results included all sizes of fish captured, including those < 200 mm TL, because these sizes were included in the catch rates reported by McAda (2002).

Length frequency. — For this study, aspects of the 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; younger individuals, in downstream reaches), and 2) sampling effort was unequal during the first two multi-year efforts (i.e., three passes in the upper reach, two in the lower) and fish from the

lower reach would therefore be under represented in a pooled sample. Hence, for these years, length frequencies from each reach are presented separately. For 2003–2005, there was an equal number of passes in the two reaches each year; length frequencies for these years were therefore displayed both separately by reach and as a combined-reach data set.

Relative year-class strength. — We assessed the relative strength of Colorado pikeminnow year-classes at age-5 by the appearance and relative abundance in the lower reach of individuals with lengths corresponding to this age (see Appendix Table I and Osmundson et al. 1997). As Colorado pikeminnow grow beyond age-5 it becomes progressively more difficult to assign age to an individual based on its length, and capturing individuals younger than age-5 appears limited by the gear types used for this study. Even using relative abundance of age-5 fish as an index to year-class strength had its problems. The incomplete record from the 2–3 year gap between multi-year sampling efforts made some year classes difficult to assess. No scale aging was done after 1992, and year classes could only be assigned based on length. 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 a group of fish of a given length range (i.e., the pulse of fish in 1991 appeared to be from one year-class but scale analysis indicated it consisted of three). 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.

Temporal variation in median length. — Tracking average length of adults in the upper reach provided another means of evaluating the relative strength of recruitment through time. 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.

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 for a fish of its length:

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

The expected mass (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 three sampling periods.

To examine whether reduced body condition might be related to increases in population abundance (i.e., a density-dependent response), we regressed our annual upper-reach abundance point estimates of fish $\geq$ 450 mm TL (independent variable) against the annual, upper-reach mean K_n of fish 500–599 mm TL (dependent variable). Regressing against the annual mean K_n of all fish $\geq$ 450 mm TL was not done because K_n varied with length and any annual changes in mean K_n could simply be related to differences in proportions of various length-classes making up the annual sample. Hence, by keeping length constant (using just 500–599 mm long fish) abundance effects on mean K_n were better isolated.

Inter-system movements. — Movement of marked Colorado pikeminnow between the Colorado and Green River systems was enumerated through visual inspection of the Colorado pikeminnow PIT-tag database maintained by the Upper Basin Recovery Program. An inter-system movement was identified when an individual fish captured in one system was later recaptured in the other system.

RESULTS

Fish Captures

There were 1,258 unique Colorado pikeminnow captured during the overall study period (i.e., all three multi-year sampling periods combined). Twenty-five passes were completed in the lower reach and 33 in the upper reach. Numbers of captures per pass per reach ranged from 11 to 73 (Table 1). There were only four fish captured in the first year that were recaptured in the last year of study (14 years apart), and these provided some interesting long-term growth information: two first captured in the lower reach and later recaptured in the upper reach, grew from 401 to 763 mm and 461 to 793 mm TL; two others, captured in the upper reach on both occasions, grew from 590 to 835 mm and 612 to 705 mm TL. Other growth rate information has been previously reported and is not summarized here (see Osmundson 2006).

Table 1. Total number of Colorado pikeminnow ≥ 250 mm TL captured in each sampling pass and year in the Colorado River study area, Colorado and Utah, 1991-2005. Totals include recaptures of the same 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
1991	37	-	-	-	-	23	17 (4)	25 (2)	-	-
1992	18	15 (1)	-	-	-	21	24 (2)	23 (2)	-	-
1993	51	41 (4)	-	-	-	31	31 (6)	33 (11)	-	-
1994	47	22 (3)	-	-	-	28	37 (3)	38 (6)	-	-
1998	31	56 (6)	-	-	-	47	73 (8)	55 (16)	-	-
1999	38	24 (2)	-	-	-	52	65 (8)	54 (18)	-	-
2000	31	19 (1)	-	-	-	51	52 (8)	28 (6)	-	-
2003	11	16 (0)	44 (0)	40 (2)	-	11	15 (0)	16 (2)	11 (1)	-
2004	28	36 (1)	27 (0)	-	-	19	16 (2)	48 (8)	-	-
2005	26	50 (3)	46 (7)	36 (6)	34 (5)	22	30 (4)	26 (4)	46 (5)	38 (9)

Model Selection

Parameters for the von Bertalanffy growth curve were estimated, with an asymptotic size of 865 mm TL (Table 2). These values were used to predict fish lengths for unobserved fish in the robust-design multi-state model. Model selection results for the robust-design multi-state analysis are shown in Table 3.

The minimum AIC_c (Akaike's Information Criterion; Akaike 1973) model {S(reach+length^2) ψ(reach*t+reach*length) p(reach*primary*t+length^2) = c DM} included a reach effect on survival (*S*) and fish total length (TL) as a quadratic model ($\beta_0 + \beta_1 TL + , \beta_2 TL^2$) but no time effect. Hence, survival is assumed constant across years, but is a function of fish total length that is identical for both reaches. The reach + time-specific model with length (i.e., year-specific survival, model {S(reach+t+length^2) ψ(reach*t+length) p(reach*primary*t+length) = c DM}) was not supported compared to the reach-only model with length, with $\Delta AIC_c = 14.14$ units greater (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- and length-specific, and when models with constant transitions were considered, all were completely unsupported with $\Delta AIC_c > 10$. Initial capture probabilities (*p*) were reach- and time-specific for both primary and secondary occasions. All competitive models for *p* included linear or quadratic models of length. Recapture probabilities within years were assumed identical to initial capture probabilities in all models considered, i.e., $p = c$. None of the models of *p* that included flow, water temperature, and number of boat days for each pass explained the temporal variation in *p* within and between primary occasions estimated with the minimum AIC_c model (Table 3). No other models of *p* were considered because of the differences in *p* within and between primary sessions.

Table 2. Estimates for the von Bertalanffy growth curve for Colorado pikeminnow in the Colorado River study area, 1991-2005.

Parameter	Estimate	Standard error	95% CI (lower)	95% CI (upper)
K	0.0666	0.00478	0.0572	0.076
L_∞	864.6	19.0188	827.2	901.9

Table 3. Model selection results of the robust design multi-state model for Colorado pikeminnow in the upper Colorado River. Survival (*S*), reach (reach), transition or movement rates between reaches (ψ), probability of capture (*p*), and fish total length (length). Other covariates considered in these models include primary and secondary occasion time effects, river flow (CFS), water temperature, and number of boat days as a measure of effort to predict capture probability. Parameters modeled with length^2 include both a linear and quadratic term for length. All recapture probabilities (*c*) were assumed equal to initial capture probabilities (*p*). The third and fourth ranked models denoted 'ADDED' are post hoc models that were developed in response to the transition analysis (see section on transitions).

Model	AICc	Delta AICc	AICc Weights	Model Liklihood	Number parameters	Deviance
{S(reach+length^2) ψ(reach*t+reach*length) p(reach*primary*t+length^2)=c DM}	8306.75	0.00	0.36	1.00	83	8133.12
{S(reach+length^2) ψ(reach*t+reach*length) p(reach*primary*t+length)=c DM}	8306.88	0.13	0.33	0.94	82	8135.43
{ADDED {S(reach+length^2) ψ(reach*t+reach*length^2 + quad spline) p(reach*primary*t+length^2)=c DM}	8308.72	1.97	0.13	0.37	87	8126.33
{ADDED {S(reach+length^2) ψ(reach*t+reach*length linear spline) p(reach*primary*t+length^2)=c DM}	8308.86	2.10	0.12	0.35	85	8130.85
{S(reach+length^2) ψ(reach*t) p(reach*primary*t+length)=c DM}	8313.56	6.81	0.01	0.03	80	8146.48
{S(reach+length^2) ψ(reach*t) p(reach*primary*t+length^2)=c DM}	8313.61	6.85	0.01	0.03	81	8144.34
{S(reach+length^2) ψ(reach*t+reach*length^2) p(reach*primary*t+length)=c DM}	8313.80	7.05	0.01	0.03	84	8137.98
{S(reach+length^2) ψ(reach*t+length^2) p(reach*primary*t+length)=c DM}	8315.17	8.42	0.01	0.01	82	8143.73
{S(reach+length^2) ψ(reach*t) p(reach*primary*t)=c DM}	8315.20	8.45	0.01	0.01	79	8150.30
{S(reach+GE(length,500)) ψ(reach*t+length) p(reach*primary*t+length^2)=c DM}	8316.84	10.09	0.00	0.01	81	8147.58
{S(reach+3 Periods+GE(length,450)) ψ(reach*t+length) p(reach*primary*t+length^2)=c DM}	8317.92	11.17	0.00	0.00	83	8144.29
{S(reach*length^2) ψ(reach*t) p(reach*primary*t)=c DM}	8318.24	11.48	0.00	0.00	81	8148.97
{S(reach+3 Periods+GE(length,500)) ψ(reach*t+length) p(reach*primary*t+length^2)=c DM}	8320.33	13.57	0.00	0.00	83	8146.69
{S(reach+t+length^2) ψ(reach*t+length) p(reach*primary*t+length)=c DM}	8320.89	14.14	0.00	0.00	89	8134.10
{S(reach) ψ(reach*t) p(reach*primary*t)=c DM}	8321.21	14.45	0.00	0.00	77	8160.65
{S(reach+GE(length,500)) ψ(reach*t+length) p(reach*primary*t+length)=c DM}	8322.33	15.58	0.00	0.00	80	8155.25
{S(reach+length) ψ(reach*t) p(reach*primary*t)=c DM}	8323.33	16.58	0.00	0.00	78	8160.61
{S(3 Periods+GE(length,450)) ψ(reach*t+length) p(reach*primary*t+length^2)=c DM}	8324.58	17.83	0.00	0.00	82	8153.14
{S(reach+3 Periods+GE(length,500)) ψ(reach*t+length) p(reach*primary*t+length)=c DM}	8325.72	18.97	0.00	0.00	82	8154.27
{S(3 Periods+GE(length,500)) ψ(reach*t+length) p(reach*primary*t+length^2)=c DM}	8327.32	20.57	0.00	0.00	82	8155.87
{S(3 Periods+GE(length,500)) ψ(reach*t+length) p(reach*primary*t+length)=c DM}	8329.94	23.19	0.00	0.00	81	8160.68

Table 3 continued.

Model	AICc	Delta AICc	AICc Weights	Model Liklihood	Number parameters	Deviance
{S(reach*t) ψ(reach*t) p(reach*primary*t)=c logit}	8330.61	23.86	0.00	0.00	93	8134.99
{S(.)ψ(reach*t) p(reach*primary*t)=c}	8332.94	26.19	0.00	0.00	77	8172.39
{S(reach) ψ(reach) p(reach*primary*t)=c}	8336.84	30.09	0.00	0.00	62	8208.61
{S(reach+length^2) ψ(reach*t+length) p(reach*mean CFS)=c DM}	8395.32	88.57	0.00	0.00	27	8340.52
{S(reach+length^2) ψ(reach*t+length) p(reach*mean CFS+length)=c DM}	8396.43	89.68	0.00	0.00	28	8339.57
{S(reach+length^2) ψ(reach*t+length) p(reach*median CFS)=c DM}	8405.85	99.10	0.00	0.00	27	8351.05
{S(reach+length^2) ψ(reach*t+length) p(reach*median CFS+length)=c DM}	8407.08	100.33	0.00	0.00	28	8350.22
{S(reach+length^2) ψ(reach*t+length) p(reach+U temperature)=c DM}	8413.89	107.13	0.00	0.00	26	8361.14
{S(reach+length^2) ψ(reach*t+length) p(reach)=c DM}	8415.13	108.38	0.00	0.00	25	8364.44
{S(reach+length^2) ψ(reach*t+length) p(reach*boat days)=c DM}	8415.90	109.14	0.00	0.00	27	8361.09
{S(reach+length^2) ψ(reach*t+length) p(reach+length)=c DM}	8416.65	109.90	0.00	0.00	26	8363.91
{S(reach+length^2) ψ(reach*t+length) p(reach*boat days+length)=c DM}	8417.61	110.85	0.00	0.00	28	8360.74

Capture Probability

Using pass 1 of 2005 as the arbitrary baseline to demonstrate the relationship for all passes in all years, capture probabilities increased with fish size up to a length of 750 mm and then declined, and capture probabilities were generally higher in the lower reach than in the upper reach (Figure 2). In both reaches, the probabilities of capturing the largest individuals were greater than the probabilities of capturing individuals < 500 mm TL. 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 3). Capture probabilities were especially low in 1992 in the lower reach and in 2003 and 2004 in both the lower and upper reaches. Capture probability was artificially high in pass three in the upper reach in 2004 (see Figure 3) as a result of additional sampling effort in July (i.e., capture effort, not considered in calculating capture probability, was substantially increased during the third pass).

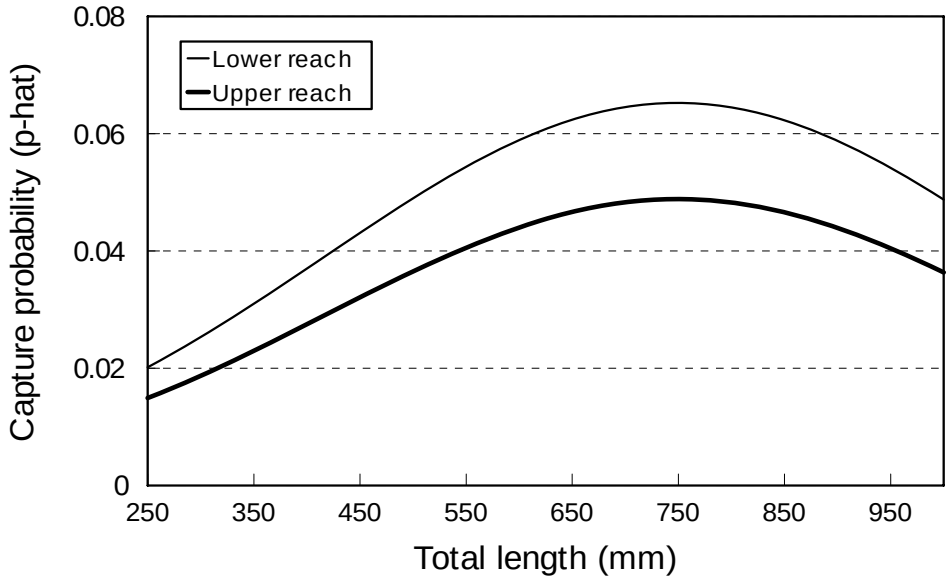

Figure 2. Capture probability for pass 1 in 2005 (arbitrarily chosen as an example to demonstrate the relationship) as a function of fish length and study reach.

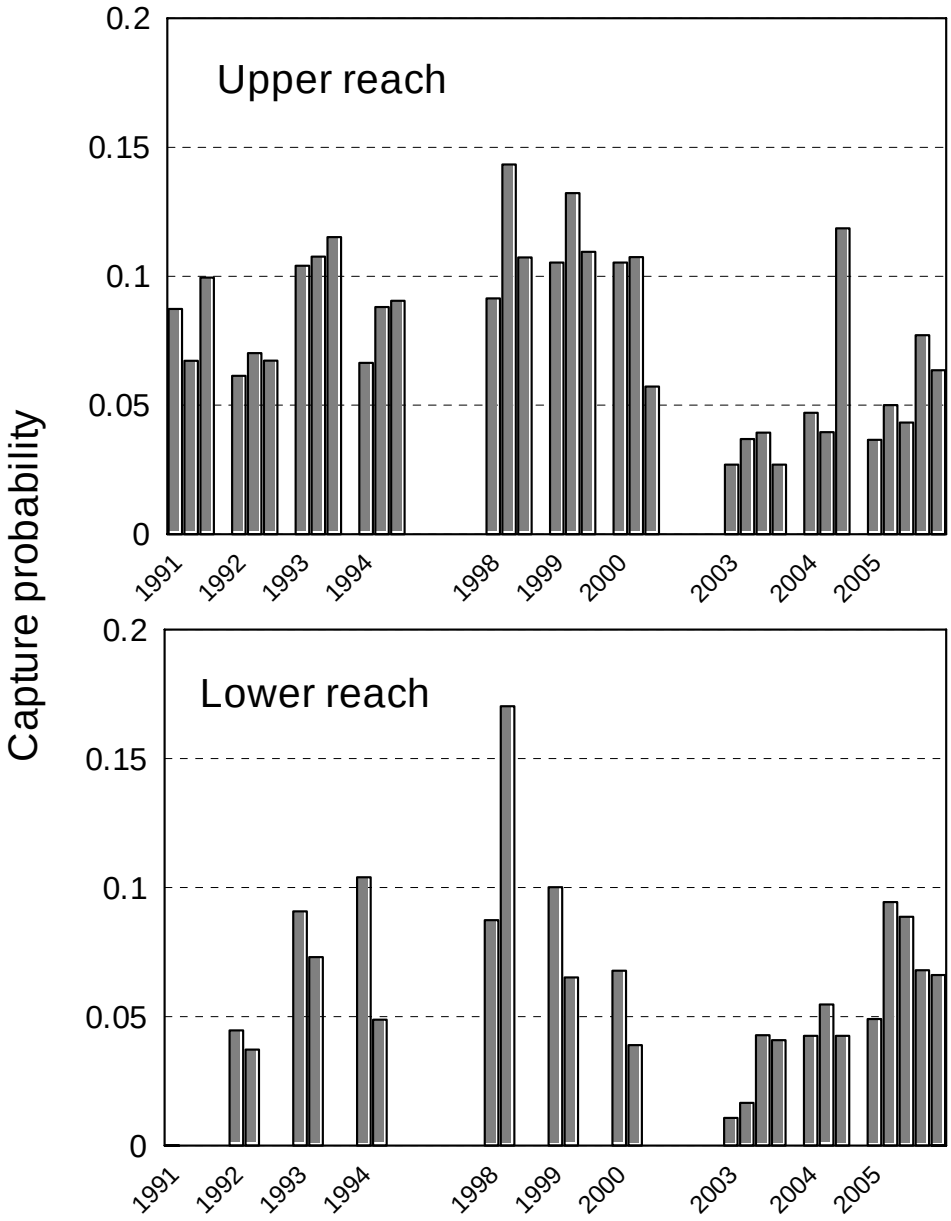

Figure 3. Capture probability by pass in the lower (top) and upper (bottom) reaches for a 500-mm-long fish. All capture probabilities included the quadratic length relationship shown in Figure 2, so that the maximum capture probability would be for fish approximately 750 mm.

Survival Rate

The effect of reach and a quadratic model of length on survival indicated that annual survival rate was consistently highest in the upper reach, and that in both reaches, survival rate increased with fish size up to a length of 550 mm, after which survival declined with additional length. The relationship was generally dome-shaped in both reaches, with a maximum plateau of 80% annual survival for fish 490–620 mm TL in the lower reach and 89% for fish 450–650 mm TL in the upper reach (Figure 4). Because the effect of length on survival was modeled as an identical additive quadratic relationship for both reaches, the model forces a constant difference in survival on the logit scale between the two reaches. Annual survival rates in the two reaches were most similar for Colorado pikeminnow 550–600 mm TL (differing by 9%), and were most dissimilar for those about 970 mm TL: (differing by 18%). These differences are a result of the constant difference between reaches on the logit scale. However, differences for the very large fish were based on extrapolation as none were actually captured in the lower reach during the entire study period. These estimated survival rates take into account fish moving from one reach to the other

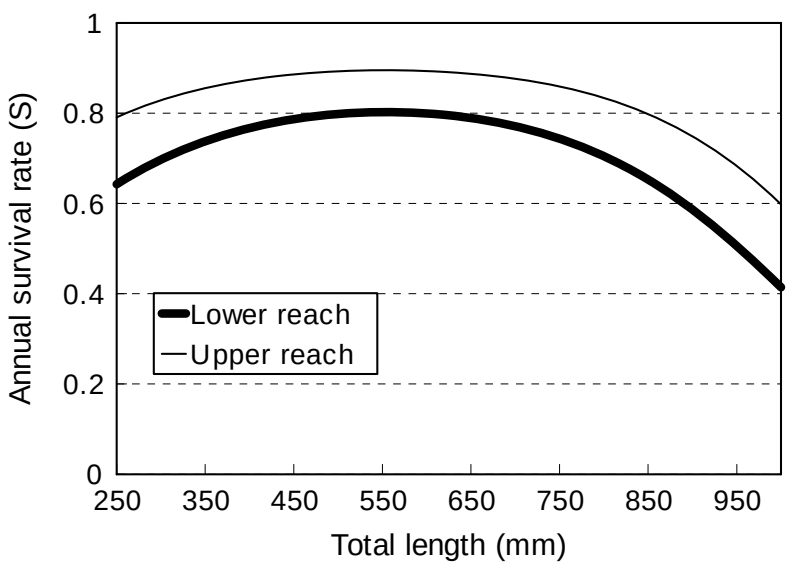

Figure 4. Annual survival rate (*S*) of Colorado pikeminnow as a function of fish total length and reach based on a model with constant annual survival, 1991–2005.

(transition probabilities), and hence, reflect actual differences in survival to the extent possible.

For fish ≥ 500 mm TL, annual survival rate was significantly higher in the upper reach (88.4%) than in the lower reach (79.8%) when survival was calculated for the entire 1991–2005 period with no length effect for fish ≥ 500 mm TL (Figure 5). Point estimates suggested a decline in annual survival rate over the three multi-year study periods both in the lower and upper reaches and when the two reaches were combined; however, differences among periods were not statistically significant. When analyzed as one river-wide population, annual survival of Colorado pikeminnow ≥ 500 mm long was estimated as 88.2% (95% CI = 85–91%) during 1991–1994, 85.9% (95% CI = 81–89%) during 1998–2000, and 80.4% (95% CI = 66–90%) during 2003–2005.

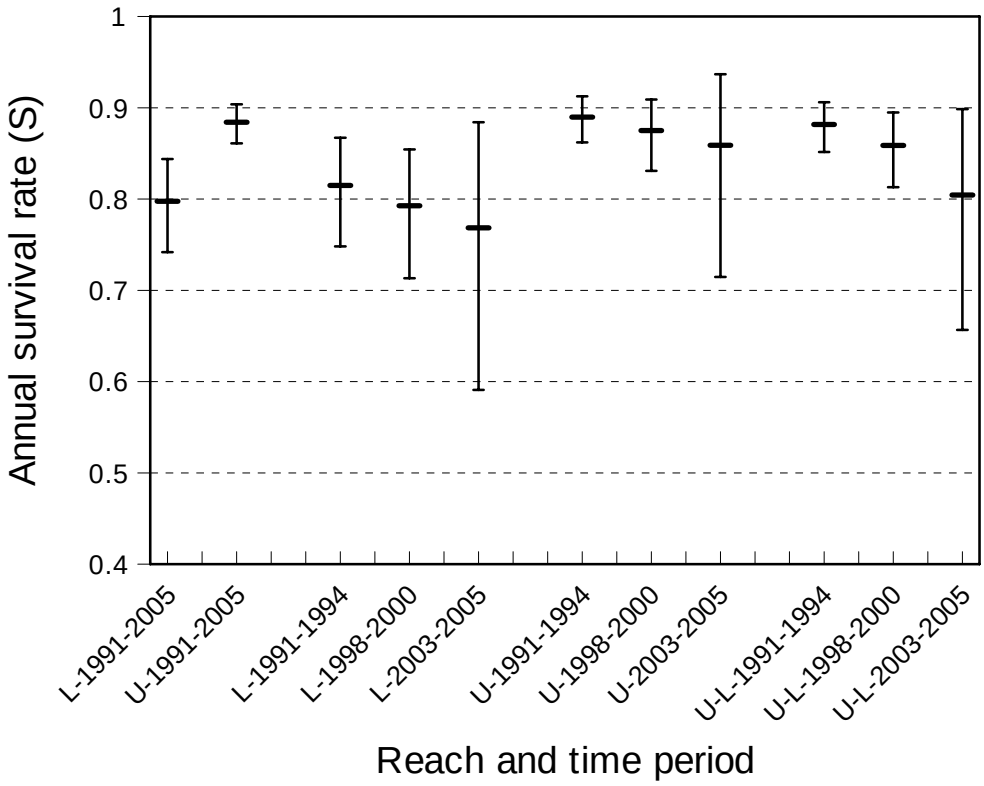

Figure 5. Annual survival rate (*S*) of Colorado pikeminnow ≥ 500 mm TL by reach (upper: U; lower: L) for the entire period 1991–2005, for the three multi-year periods, and also for the two reaches combined (U-L) during each of the multi-year periods.

Population Size

Annual abundance estimates for the four length groups of Colorado pikeminnow in the two reaches, and for the two reaches combined are provided in Appendix tables I–IV. 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 402 (1998) to 1,192 (2003) and for the upper reach, from 217 (1991) to 484 (2005); summed estimates ranged from 772 (1992) 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 those fish ≥ 500 mm TL, estimates ranged from 75 (1992) to 297 (2003) in the lower reach and from 175 (1993) to 399 (2005) in the upper reach; summed estimates ranged from 334 (1992) to 656 (2005).

Regardless of the length group, summed point estimates were lowest in 1992 and highest in 2005. The narrowest confidence intervals were for fish ≥ 500 mm TL. However, for all length groups, differences among annual estimates were not statistically significant as evidenced by overlapping confidence intervals (Figure 6). Precision of annual estimates was generally higher (lower CVs) for the upper reach than for the lower reach (Appendix tables I-III). For all three length groups described above, six of nine annual CVs for the summed-reach estimates were < 20% and the most precise estimates were in 2005 (CV range of 9.4-10.4).

Slopes of lines fitted to the 'shrunk' estimates derived from the variance components trend analysis indicated the adult population significantly increased during the 1992–2005 study period. For fish ≥ 450 mm TL, 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 ≥ 500 mm TL (slope: 10.29/year; SE: 3.36; Wald chi-square: 9.4; $P = 0.002$). Slopes reported are estimated increases of fish per year.

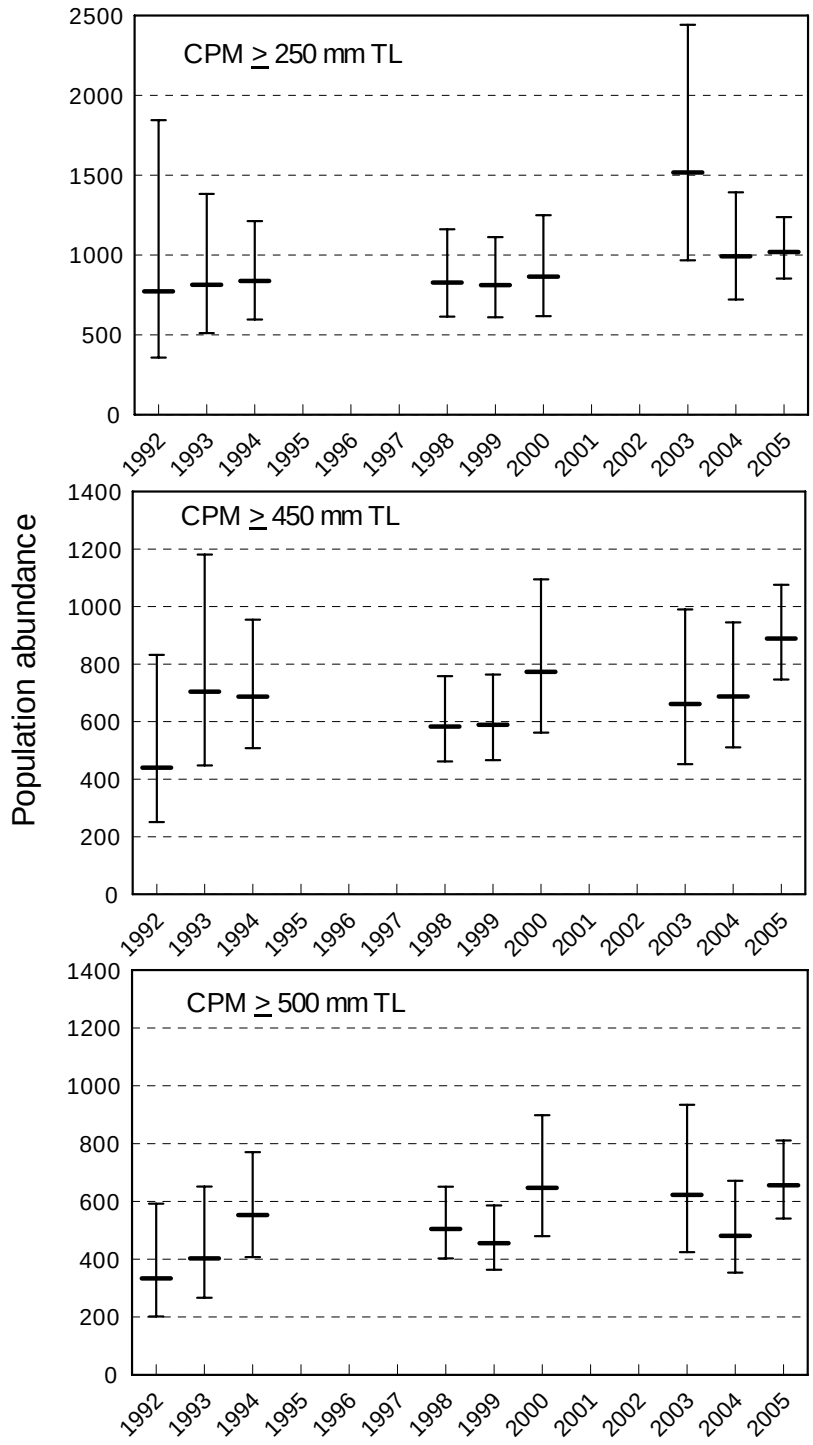

Figure 6. Abundance estimates of Colorado pikeminnow of three sizes classes: ≥ 250 mm TL; ≥ 450 mm TL; ≥ 500 mm TL in the upper Colorado River study area (reaches combined), 1992–2005. Annual population abundance estimates shown were derived by summing separate estimates for the lower and upper reaches (see Appendix Tables II, III and IV for numbers).

Temporal changes in abundance of all fish (≥ 250 mm TL) did not appear to be synchronized between the two reaches as evidenced by annual changes in point estimates (Figure 7). Explanations for why this might be can be found in sections below that describe differences in length frequency between the two reaches and movement of fish between the reaches.

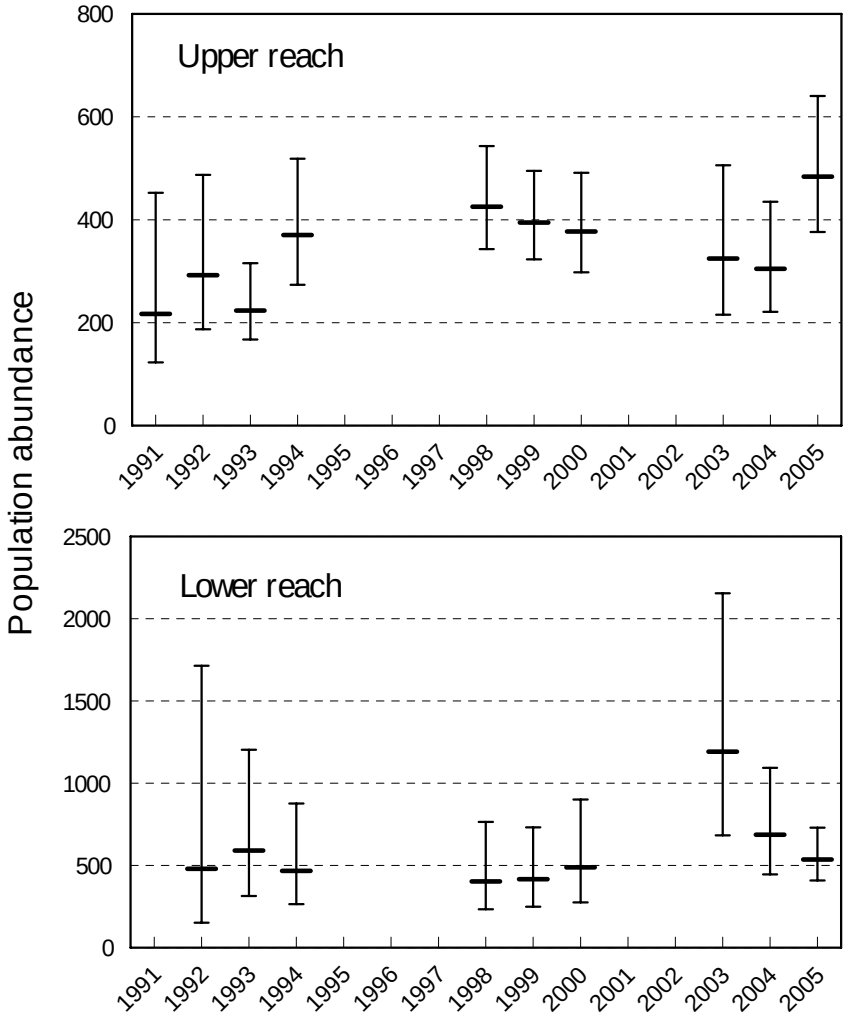

Figure 7. Abundance estimates of Colorado pikeminnow ≥ 250 mm TL in the upper (top) and lower (bottom) Colorado River study reaches, 1991–2005 (see Appendix Tables I, II and III for numbers).

Population Replacement

Abundance estimates of fish 400–449 mm TL (Recovery Goals criterion for fish about to recruit) in the two reaches indicated the bulk of these fish were in the lower reach (Figure 8). There, annual estimates ranged from 23 to 248; in the upper reach, 1 to 12. Because this length group is a fairly small subset of the total population, captures and recaptures were limited, resulting in wide confidence intervals around $\hat{N}$, large standard errors, and CVs greater than the recommended 20% (Appendix Table IV). Estimates from the upper reach were especially imprecise.

Despite this imprecision, the combined-reach abundance estimates along with mortality rate estimates provided 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%. Results indicated a gain of fish $\geq$ 450 mm TL in six of the nine years studied, ranging from 1 to 143 additional individuals per year (Figure 9). Annual losses ranged from 35 to 119 individuals per year. The estimated net gain for the nine years studied was 332 fish $\geq$ 450 mm TL. Because estimates were not available for 1995–1997, 2001, and 2002, total gain or loss for the 14-year period could not be estimated.

Ability to Detect Change in Abundance

Using CVs typical of those encountered during the study, we calculated the percent decline that would be required for the decline to be significant at $\alpha = 0.05$ and $\alpha = 0.10$. The overall mean CV of the nine annual combined-reach estimates for fish $\geq$ 450 mm TL was 18.0%. During the last three-year effort (2003–2005) considerable sampling effort was expended, including the addition of post-spawning captures from another study in two of the three years. This improved the mean CV over that of the first three-year effort, but not the second three-year effort: mean CV for the first three years was 25%; for the second three years, 14.3%; for the last three years, 15.2%.

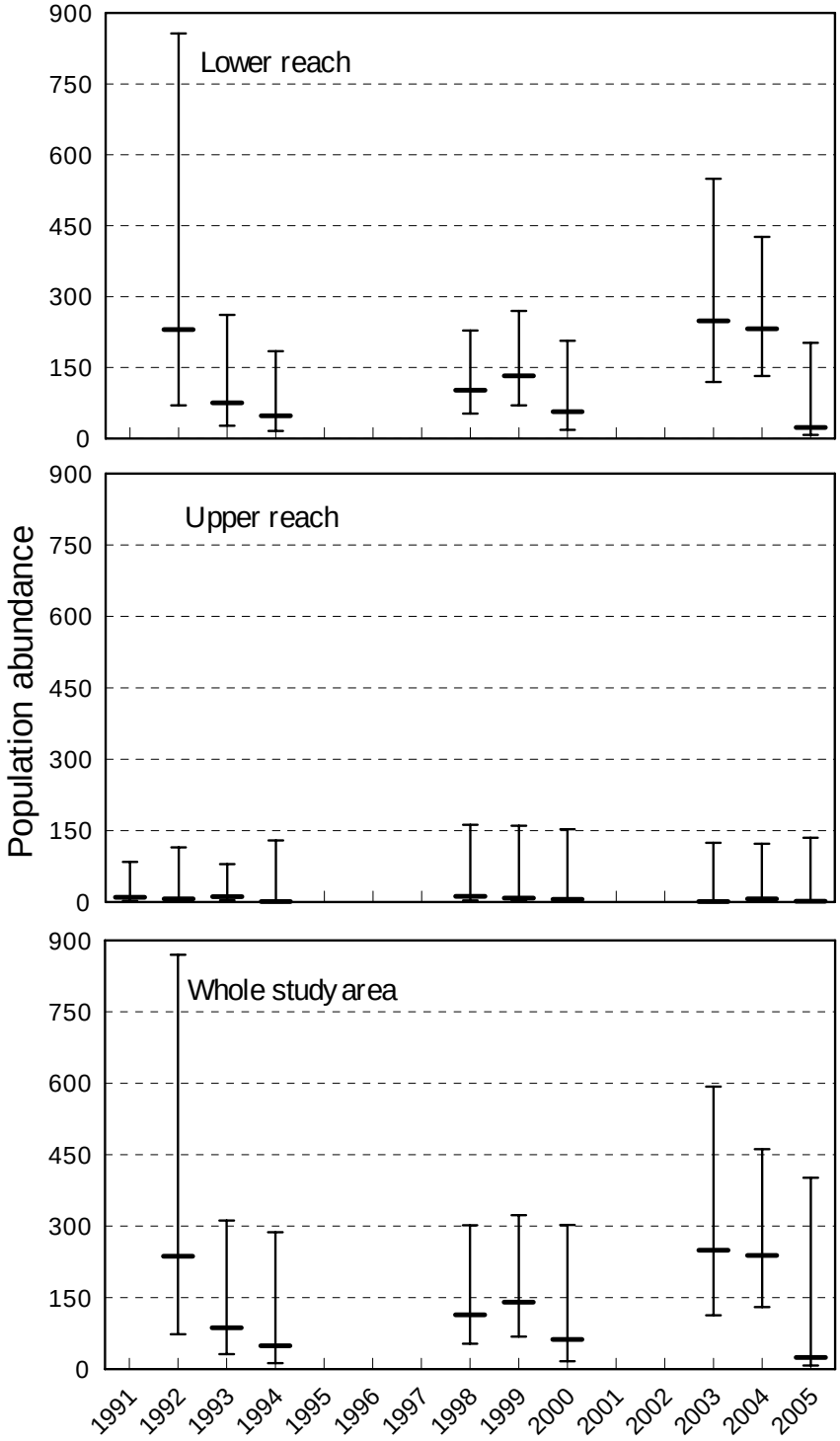

Figure 8. Annual abundance estimates of Colorado pikeminnow 400–449 mm TL in the lower, upper and combined reaches, 1991–2005.

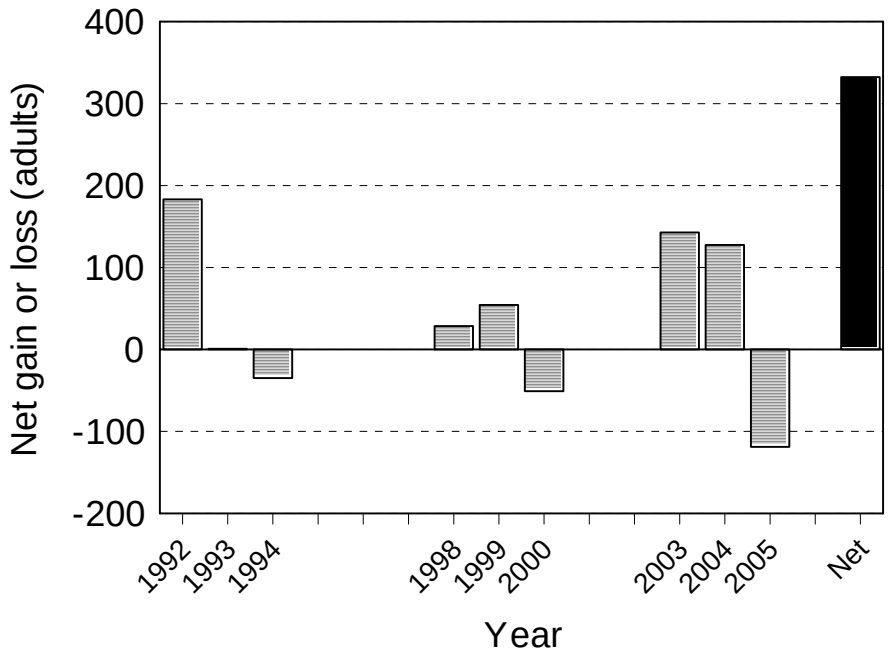

Figure 9. Annual net gain or loss of Colorado pikeminnow ≥ 450 mm TL in the summed-reach population based on the estimated number of fish 400–499 mm TL present each year minus the estimated number of deaths of fish ≥ 450 mm TL.

With a CV of 18%, $\hat{N}_1$ would have to decline by 35.2% for it to be significant at α = 0.05, and 28.3% at α = 0.10 (Figure 10 and Appendix Table V). With a CV of 15%, $\hat{N}_1$ would have to decline by 30.1% for it to be significant at α = 0.05, and 24.1% at α = 0.10. For our earliest mean CV value of 25%, $\hat{N}_1$ would have to decline by 46.6% for it to be significant at α = 0.05, and 37.7% at α = 0.10. Finally, the smallest CV, 9.4% was in 2005, the year we completed five passes in each reach, with the fifth upper-reach pass consisting of post-spawning captures. For two annual abundance estimates with this CV, $\hat{N}_1$ would have to decline by 19.8% for it to be significant at α = 0.05, and 15.7% at α = 0.10.

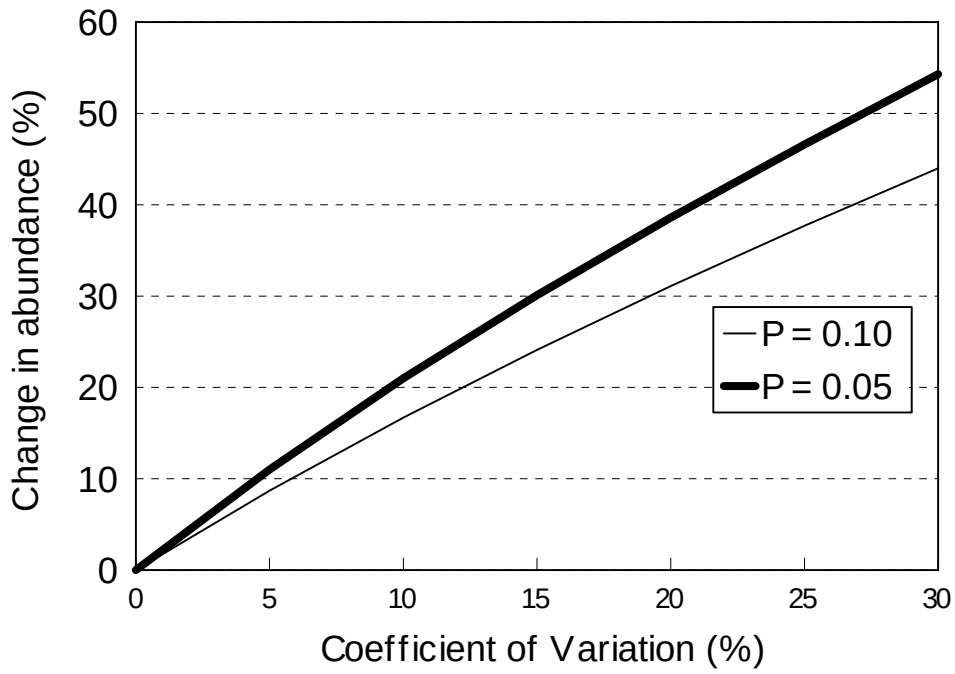

Figure 10. Relations between coefficient of variation (100 x SE/ $\hat{N}$) and percent change in population abundance required for a change to be detected at α = 0.05 and at α = 0.10.

Transition Probabilities

As previously reported, 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 (Osmundson et al. 1998). Overall, we documented 48 movements from the lower to the upper reach 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. However, the probability that a fish would make a between-reach movement 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. Based on the probabilities calculated, there appeared to be no between-

reach movements in two of the one-year intervals, a net upstream movement in at least five of the one-year intervals, and a net downstream movement in at least two of the one-year intervals (Table 4).

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 4). 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 (2003 to 2004 and 2004 to 2005) probabilities of movement to the lower reach were again 0%.

When the top model (minimum AIC_c) for generating survival and abundance estimates 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 10 cases in which the recapture in the upper reach occurred one year after the initial capture in the lower reach, the smallest individual when

Table 4. Annual (1991–2005) 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

[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 if capture data were available.
[2] Average per year calculated from single value for period 1998-2000.

captured in the lower reach (before having moved) was 402 mm TL (Table 5), suggesting that few smaller individuals made the lower-to-upper reach transition. Two additional post hoc models were developed to provide a more biologically realistic relation between length and transition, or at least one more consistent with the empirical data (Figure 11). Both linear and quadratic spline models were fitted to the transition probabilities, with cutpoints at 400 mm for ψ^{LU} and 500 mm for ψ^{UL}. For ψ^{LU}, the additional cutpoint variable is the total

Table 5. 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; rk = river kilometers from the confluence; GU = Gunnison River.

	Lower reach capture			Upper reach capture		
Fish ID number	Year	Location (rk)	Length (mm)	Year	Location (rk)	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

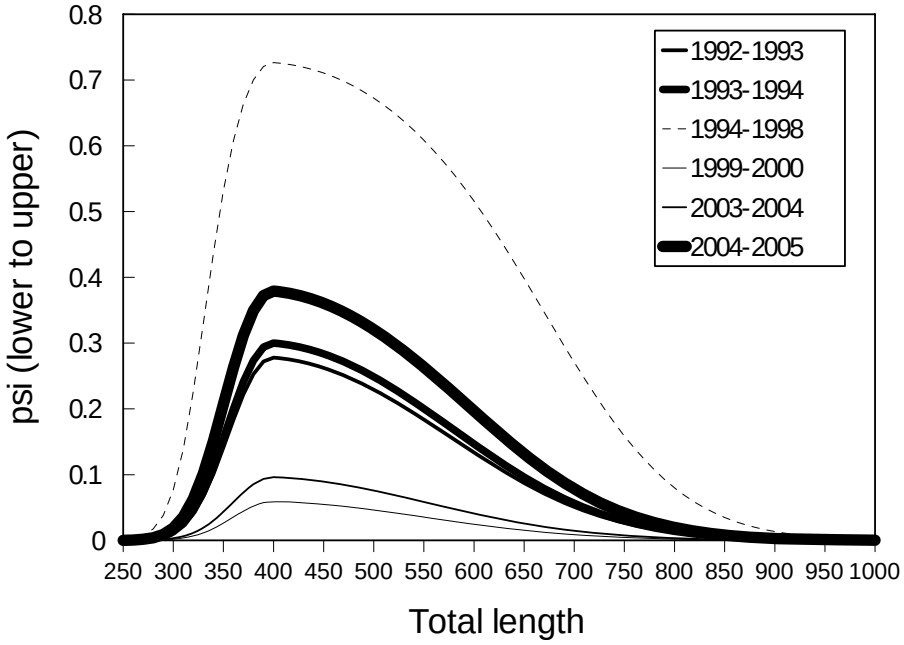

Figure 11. Transition (movement from the lower reach to the upper reach of the Colorado River study area) probabilities of Colorado pikeminnow as a function of total length (mm) as estimated using a quadratic spline model with cutpoints at 400 mm. Only intervals in which transitions occurred are shown. The dotted line indicates probabilities of transition during the four-year interval of 1994-1998 when sampling was curtailed for three years; other lines (solid) indicate probabilities of transition during one-year intervals.

length minus 400, but with all negative values taken as zero. For ψ^{UL}, the additional cutpoint variable is the total length minus 500, with all negative values taken as zero. The linear spline model was identical to the minimum AIC_c model of Table 3, but with these two cutpoint variables added. The quadratic spline model included a quadratic model of length for both ψ^{LU} and ψ^{UL} plus the squared values of the two cutpoint variables. Because of the small number of fish that made transitions and the four additional parameters in the quadratic spline compared to the minimum AIC_c model, this quadratic spline model {S(reach+length^2) psi(reach*t+reach*length^2 + quad spline) p(reach*primary*t+length^2)=c DM} did not improve AIC_c of the current top model and thus was not used for estimating abundance or survival.

Electrofishing Catch-per-Effort

Mean catch rates were relatively low during 2003–2005. There was some variation among passes within years, but most differences were not significant (Figures 12–14). The mean pass catch rate in both reaches was < 0.5 fish/hr except in 2005 when the upper-reach, pass-4, catch rate was 0.8 fish/hr. There was no consistent trend of catch rates either increasing or decreasing within years as spring sampling progressed.

Mean catch rates for the entire study area (passes and reaches combined) progressively increased from 2003 to 2005 (Figures 12–14, bottom panels). The mean catch rate in 2005 (0.43 fish/hr) was significantly greater than the mean in 2003 (0.21 fish/hr). Mean catch rate in the lower reach (0.33 fish/hr) was almost identical to the mean catch rate in the upper reach (0.32 fish/hr) when data from all three years were pooled by reach (not shown).

Mean catch rates within ISMP river segments were very similar to those within the larger study area (Figures 12–14, top, middle, bottom). Only in 2004 did catch rates in the ISMP upper-reach segment appear to differ from the entire upper reach (lower catch rates in all passes), but differences were not significant (Figure 13, top). When data from the whole study area (upper and lower reaches) were pooled, ISMP results closely matched the larger data set.

As reported by McAda (2002), mean ISMP catch rate (ISMP river segments combined) fluctuated around 0.25 fish/hr during 1986–1990 and increased to about 1.0

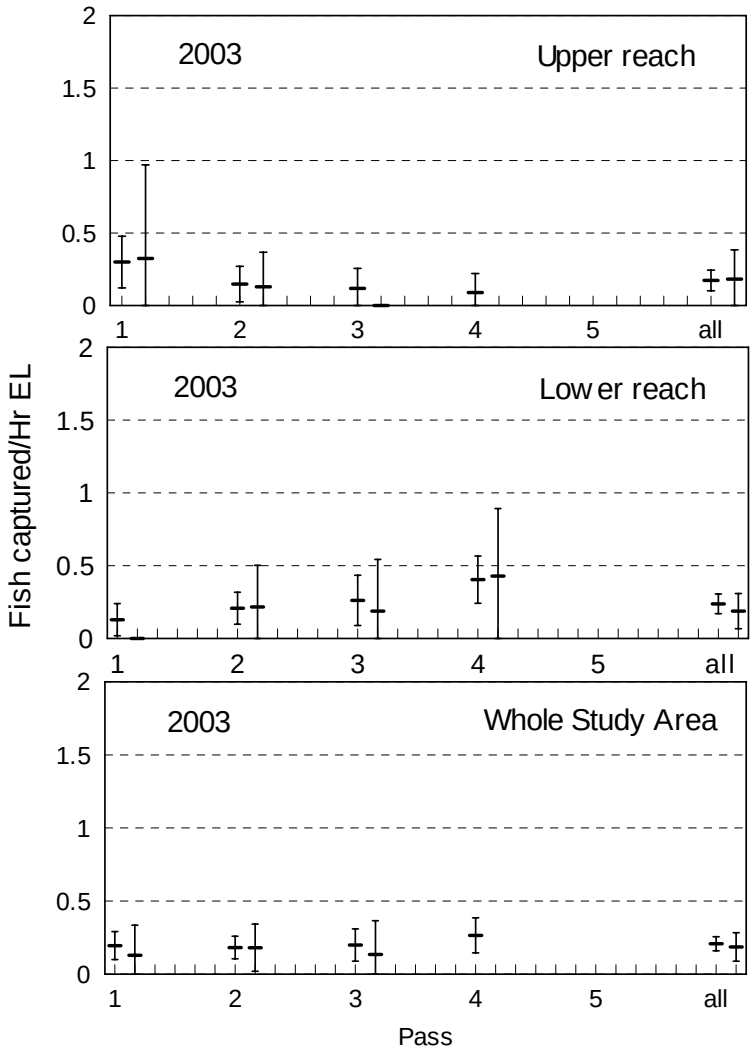

Figure 12. Electrofishing catch rates (fish per hour) of Colorado pikeminnow in the upper reach (top), lower reach (middle), and whole Colorado River study area (lower) during sampling passes of 2003. For each pass, catch rates of entire shorelines (left bar) and catch rates of shorelines from ISMP sub-reaches only (right bar) are displayed. Also shown are catch rates when captures and effort from all passes were combined (all).

fish/hr during 1992–1998. It then declined to 0.62 in 1999 and 0.34 fish/hr in 2000 (Figure 15-bottom). Mean catch rate in five of the seven years during 1992–1998 was significantly higher than in all five years of 1986–1990. Mean catch rate in 2000 was significantly lower than the mean of 2000. Confidence intervals around the 2003–2005 means were narrower than previous ISMP means because the multiple passes provided larger annual sample sizes.

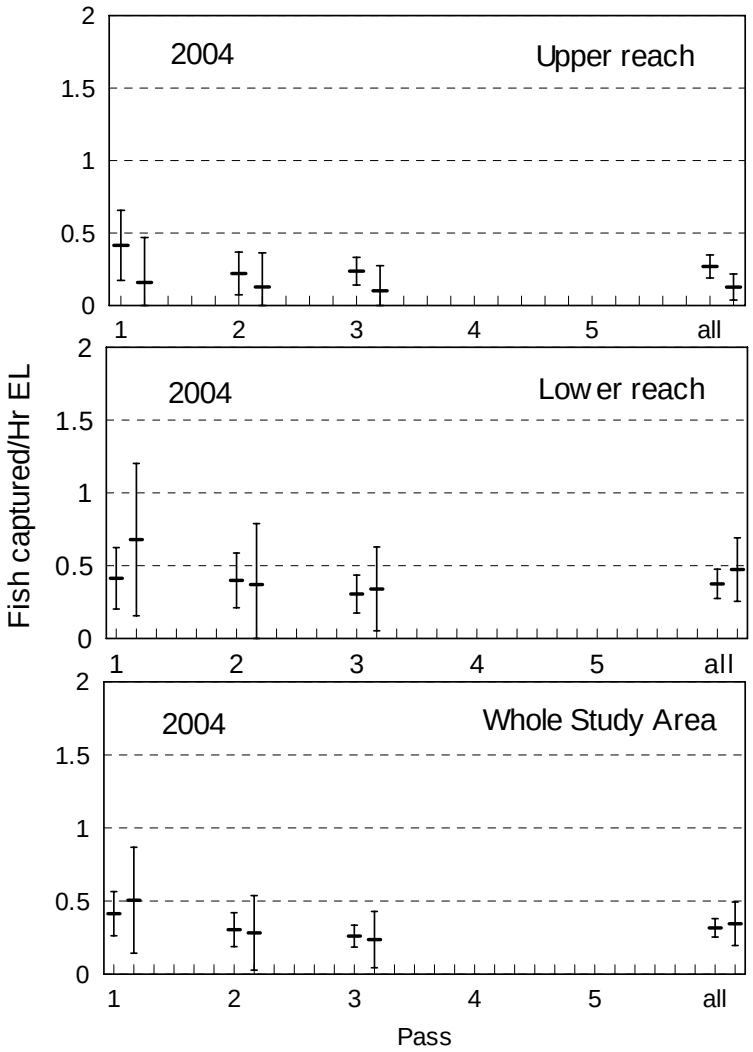

Figure 13. Electrofishing catch rates (fish per hour) of Colorado pikeminnow in the upper reach (top), lower reach (middle), and whole Colorado River study area (lower) during sampling passes of 2004. Explanation provided in Figure 12 caption.

When mean annual catch rates of 1986–2005 (river segments combined) were regressed with year (no values for 2001 and 2002), no temporal trend was evident ($r^2 = 0.04$; $P = 0.43$), i.e., there was no lasting increase in mean catch rates from beginning to end of the period even though rates clearly increased during the middle of the period (Figure 16-top). Electrofishing catch rates may, however, have been biased low during the 2003-2005 sampling efforts (see Discussion); when these mean annual catch rates were removed from the regression analysis (Figure 16-bottom) a significant upward trend was indicated ($r^2 = 0.33$; $P = 0.02$).

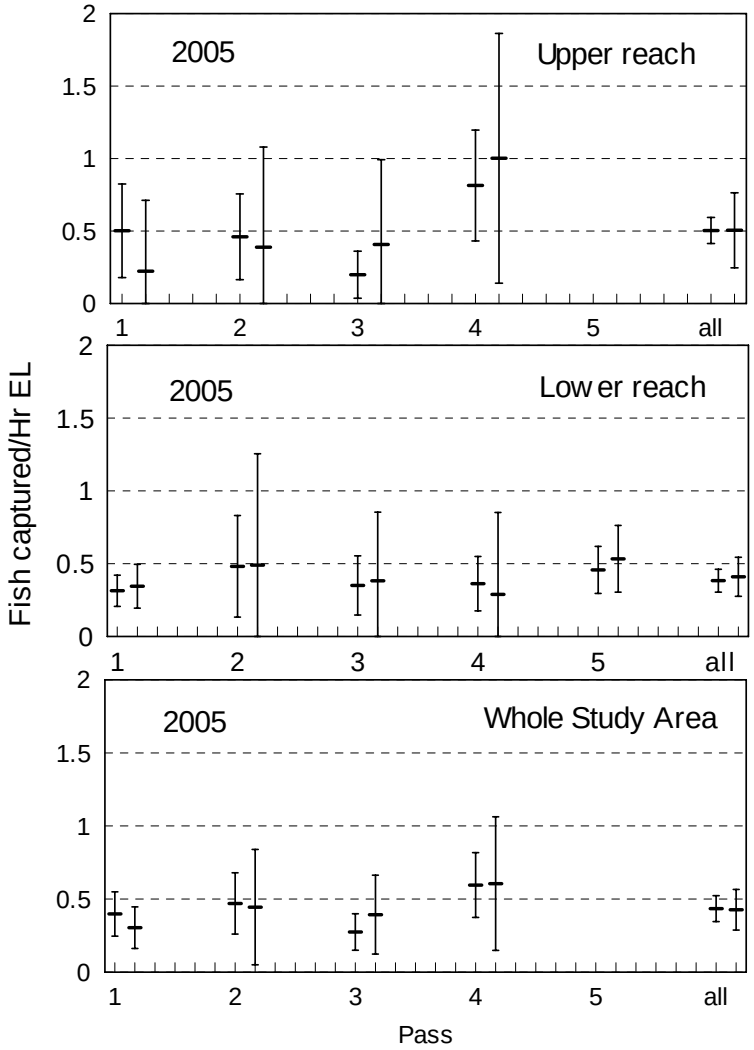

Figure 14. Electrofishing catch rates (fish per hour) of Colorado pikeminnow in the upper reach (top), lower reach (middle), and whole Colorado River study area (lower) during sampling passes of 2005. Explanation provided in Fig. 12 caption. In 2005, catch-per-effort was not documented during pass 5 in the upper reach (captures were from an unrelated nonnative fish removal program).

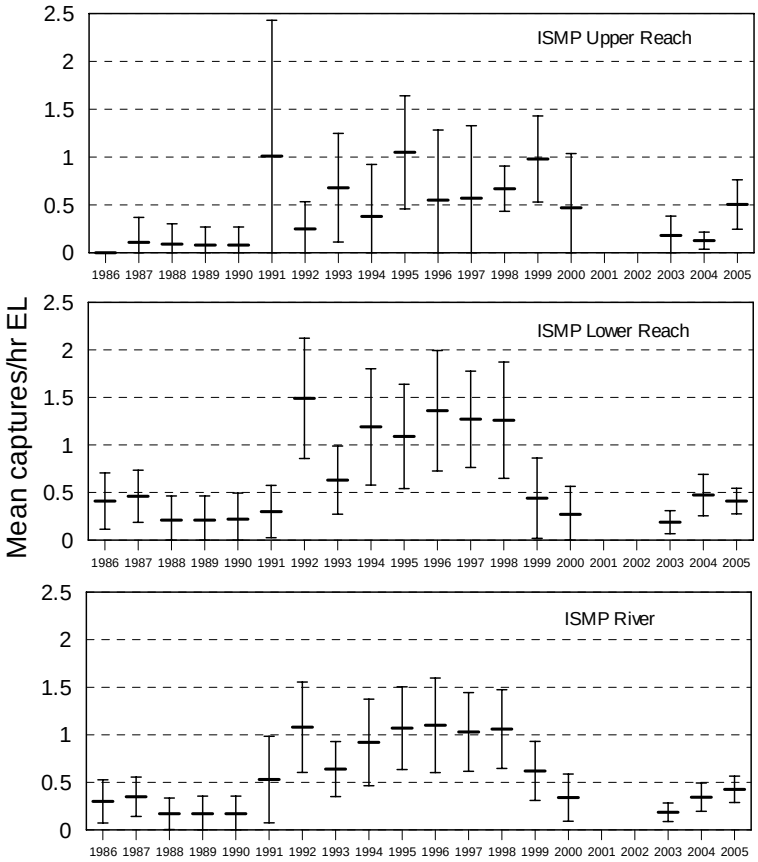

Figure 15. Interagency Standardized Monitoring Program (ISMP) electrofishing mean catch rates (fish/hr) of Colorado pikeminnow in the upper (top), lower (middle), and combined (bottom) ISMP reaches of the Colorado River study area, 1986–2005. For years 1986–2000, one pass was made along both shorelines of each sampling segment within each reach (McAda 2002); for years 2003–2005 (this study), only capture rates within the ISMP sampling segments are shown, and rates reflect the combined results of 3–5 electrofishing passes through each segment per year. Error bars represent the 95% confidence interval about the mean.

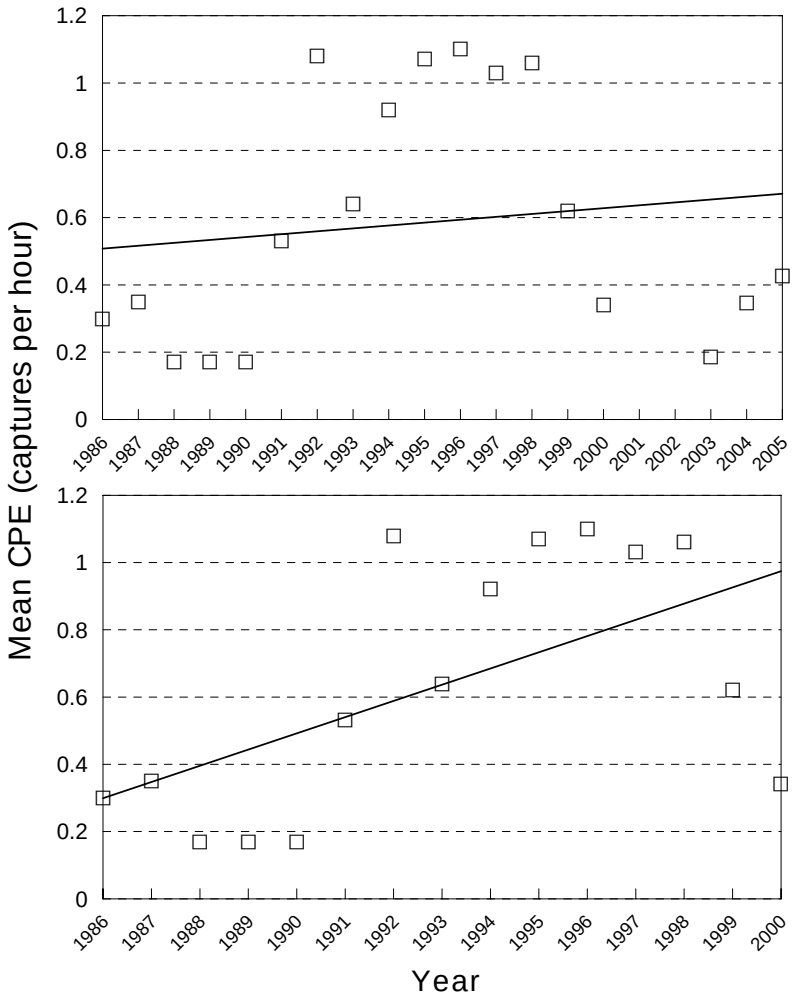

Figure 16. Linear regression of electrofishing capture rates (fish/hr) of Colorado pikeminnow in the Colorado River study area and year of capture. Top graph includes 1986–2005 results (see Figure 15-bottom; no results for 2001 and 2002); bottom graph includes only 1986-2000 results.

Length Frequency

Although abundance estimates and capture rates provide insight into intermediate-term population trends, the high variance associated with these estimates limits understanding of short-term population dynamics. Examination of length-frequency histograms can be useful in providing additional information including recruitment history.

Years 1991–1994 & 1998–2000. — In the first year of study, 1991, almost all Colorado pikeminnow captured in the lower reach were juveniles 310–400 mm TL, and most

of these were 340–380 mm TL (Figure 17). As reported by Osmundson and Burnham (1998), scale analysis indicated this pulse of young fish primarily consisted of three year-classes, 1985, 1986 and 1987, with the 1986 year-class occurring most frequently in samples. These cohorts dominated the lower reach subpopulation during 1991–1994. Length data indicated fish younger than the 1985–1987 year-classes were beginning to appear by 1994, but there was no obvious spike in abundance of any one length-class that might suggest a strong year-class. In 1991, there was a scarcity of fish ≥ 500 mm TL in the lower reach: only one was captured (560 mm), or 3% of the lower-reach sample (n = 37). A similarly small sample in 1992 (n = 32) also yielded few individuals ≥ 500 mm TL (19% of captures). By 1993 and 1994, many fish from the 1985–1987 year-classes had reached this size: in 1993, 40% of the lower reach sub-population was ≥ 500 mm TL; in 1994, 56%.

During 1998–1999, juvenile-sized fish again comprised much of the lower-reach subpopulation, but their length-frequency distributions were not strongly bell-shaped as in 1991–1994 (Figure 18). However, in 1998, individuals between 330 and 450 mm TL were relatively abundant (45% of the subpopulation). Judging from their size, many of these fish were likely age-5 (see Osmundson et al. 1998), suggesting that 1993 may have produced a relatively strong year class. Individuals ≥ 500 mm TL made up 32% of the subpopulation in 1998 and 28% in 1999. By 2000, many of the juveniles present in the two previous years had grown to ≥ 500 mm TL, and with few new juveniles, these larger fish made up 65% of the lower-reach sample. The relatively low number of individuals 250–449 mm TL (ages 4 and 5) suggests that 1995 and 1996 were weak year classes.

In the upper reach, fish < 460 mm TL comprised 0–5% of the sampled population during 1991–1994 and 1998–2000 (Figures 19 & 20), indicating that few fish in the upper reach were reared there and that when individuals moved to the upper reach from the lower reach, they evidently did not do so until they were in the mid-400 mm range or longer (discussed later).

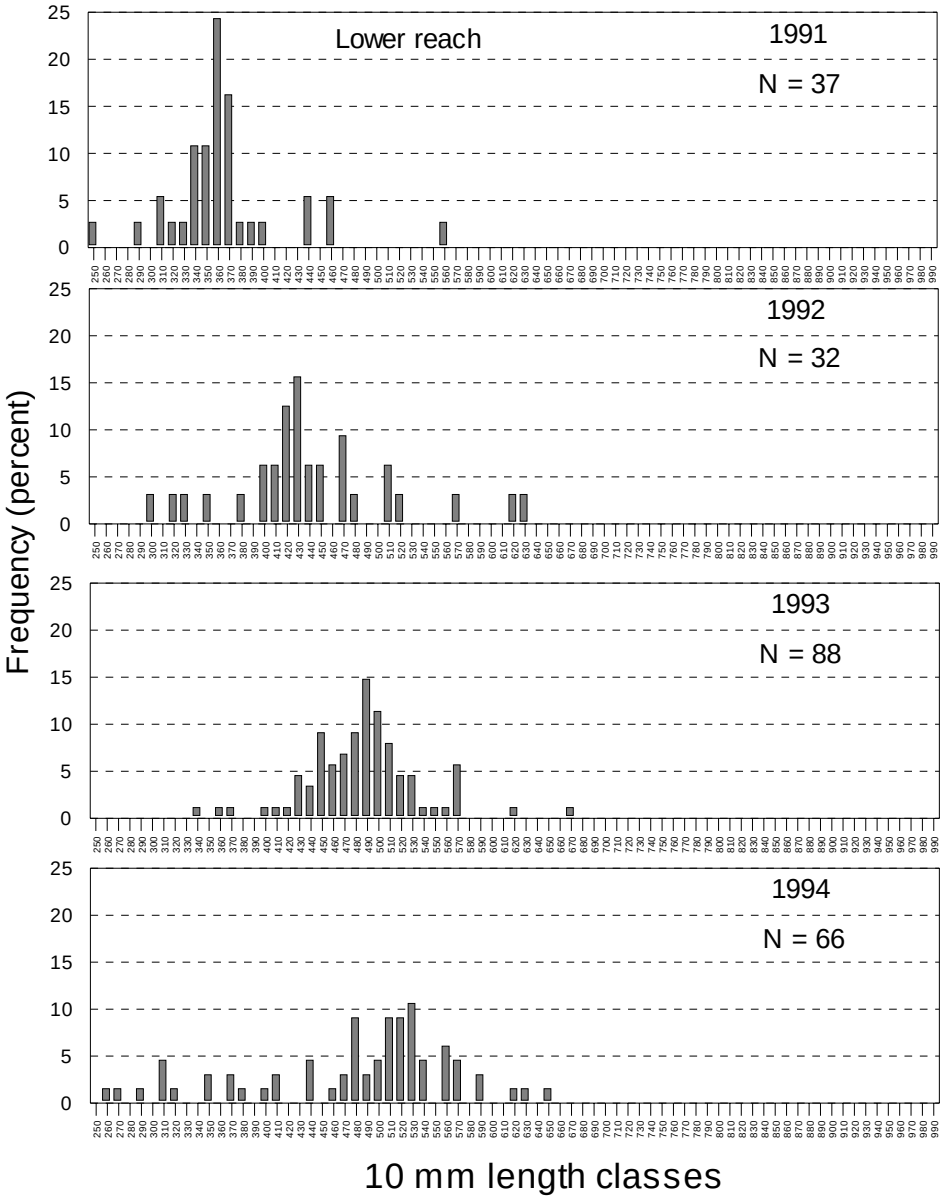

Figure 17. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 1991–1994.

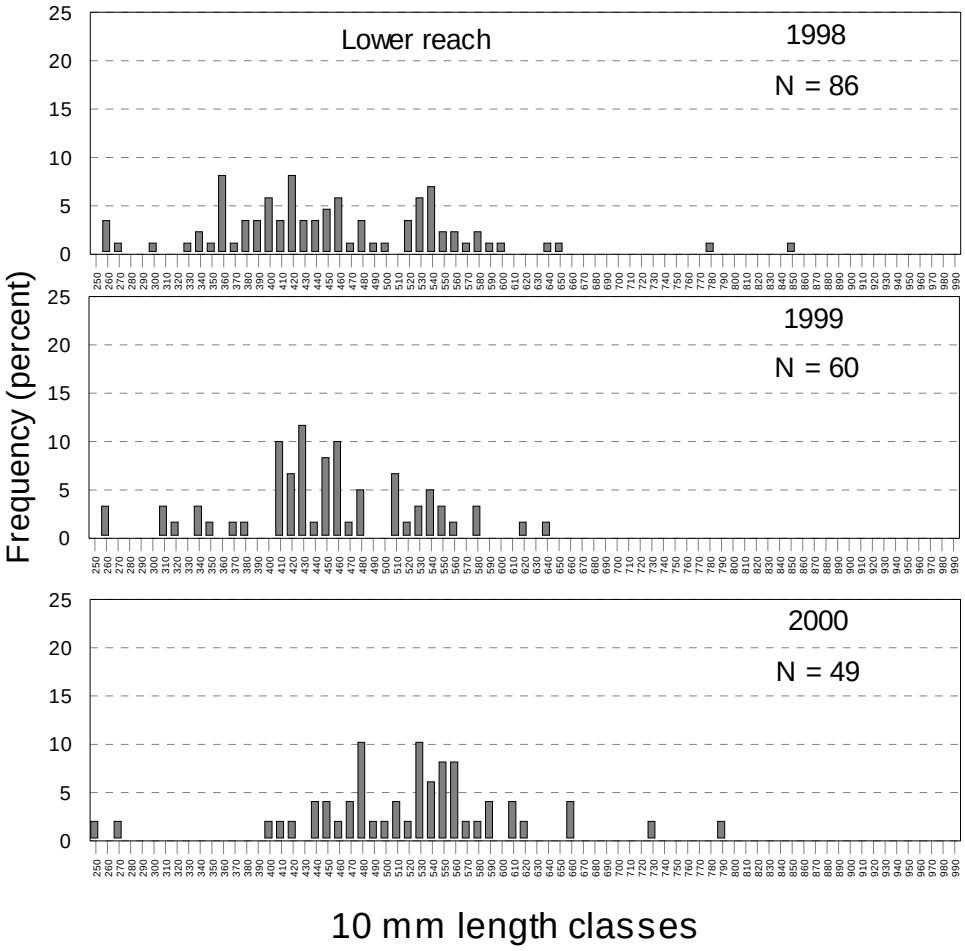

Figure 18. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 1998–2000.

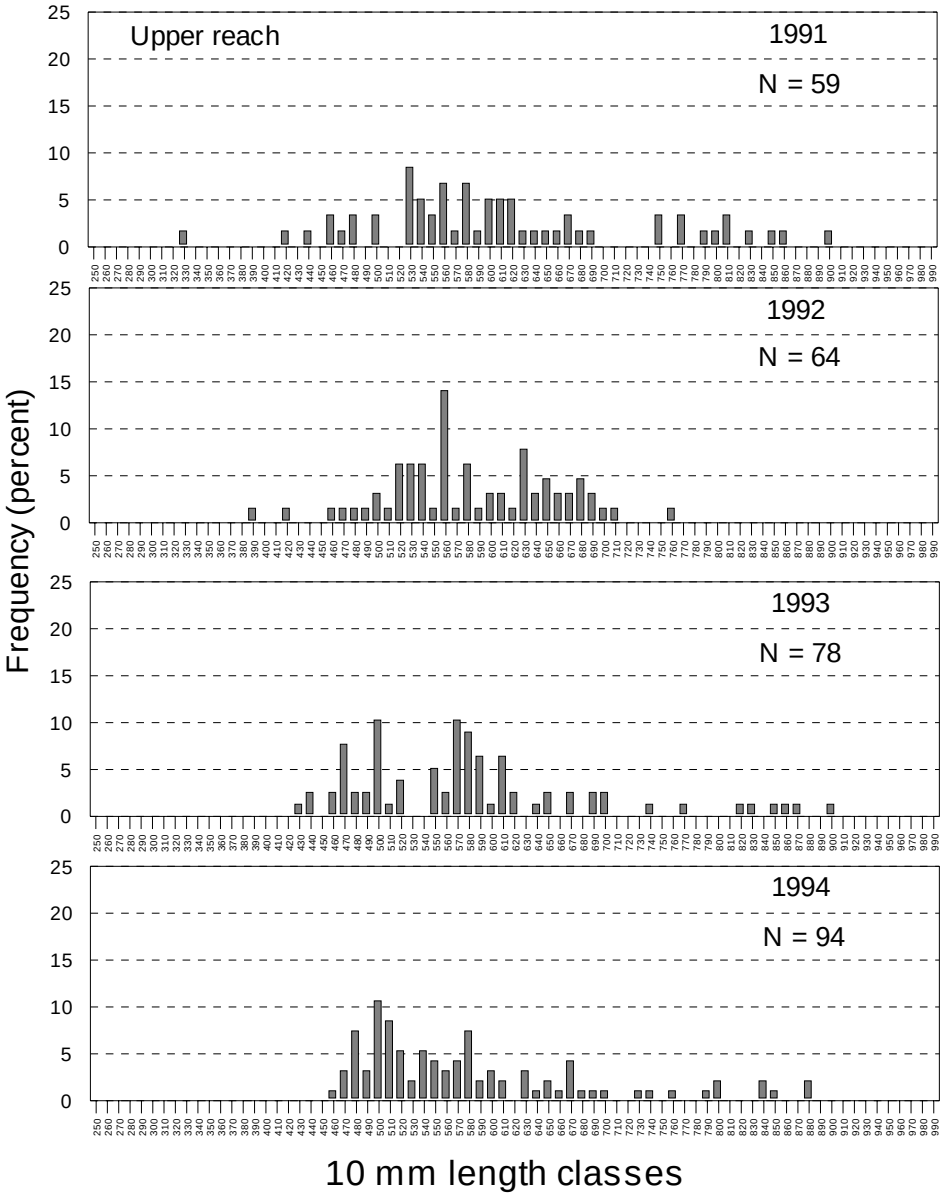

Figure 19. Length frequencies of Colorado pikeminnow captured in the upper Colorado River study reach, 1991–1994.

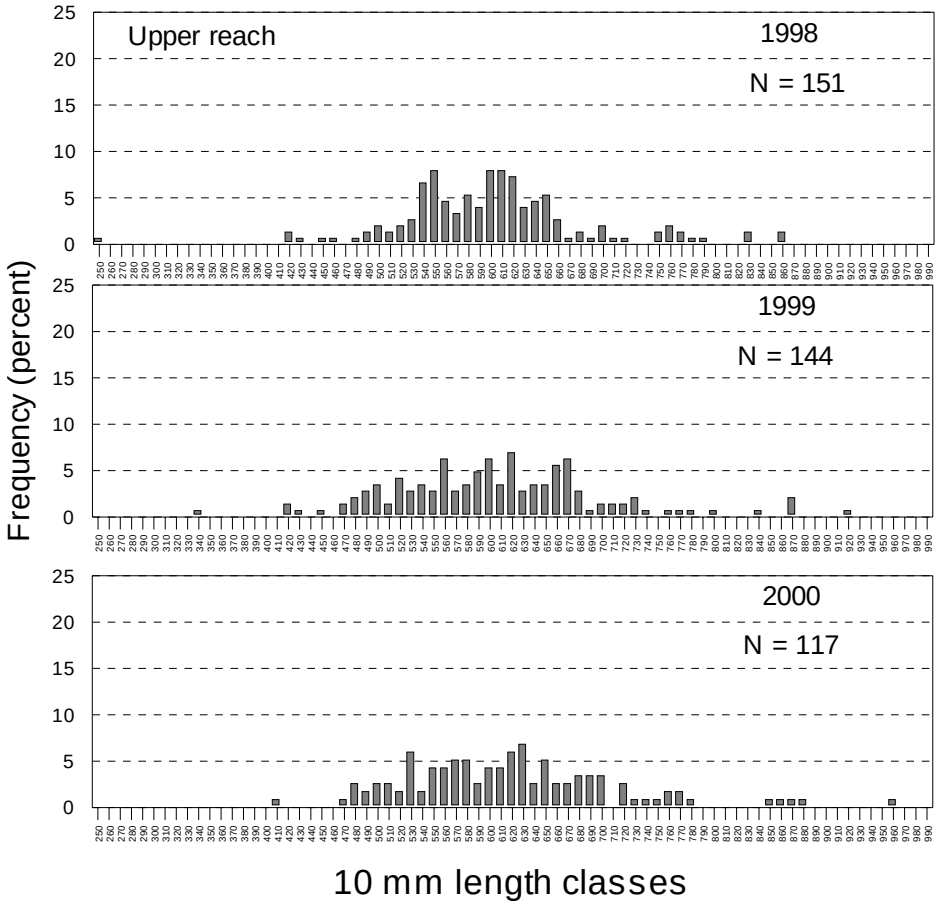

Figure 20. Length frequencies of Colorado pikeminnow captured in the upper Colorado River study reach, 1998–2000.

Temporal variation in median length -- A constant median length from year to year would be expected if recruitment and adult mortality were consistent and balanced each year. However, as the length-frequency data from the lower reach indicates, Colorado pikeminnow recruitment often comes in pulses, with only some years producing strong year-classes. A drop in the median length of adults in the upper reach, as observed in the early 1990s (Figure 21), results from an infusion of young recruits to the adult population, i.e., numbers of small adults entering the population are great enough to offset the effect that growth of older adults has 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 infusion of small adults had dropped off during the intervening (non-sampled) years of 1995–1997. This increase in median length continued through 2000, indicating that fish growth was having a greater effect on the

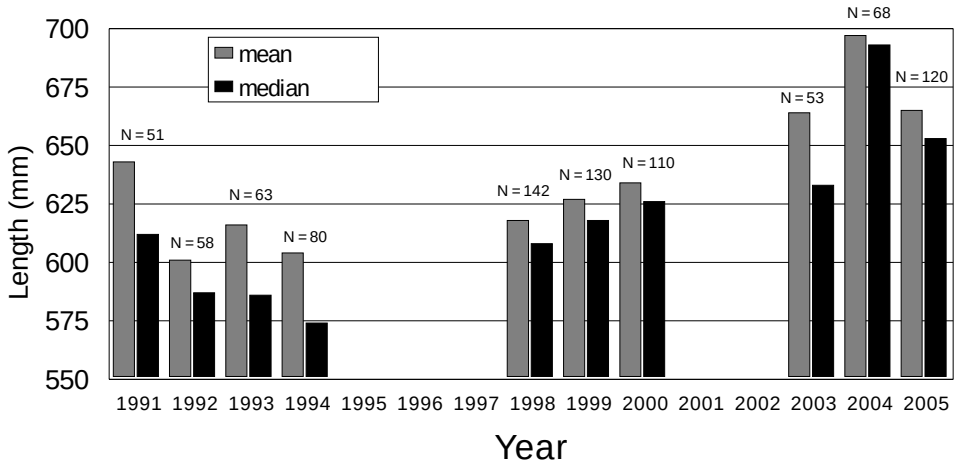

Figure 21. Mean and median lengths of Colorado pikeminnow captured in the upper Colorado River study reach, 1991–2005. N = sample size.

median than did the infusion of young adults. It should be noted that upper-reach abundance could theoretically remain constant or even increase during periods of low recruitment in the lower reach if adults from the lower reach continued to emigrate upstream at a rate equal to or higher than that of upper-reach adult mortality. In fact, upper-reach abundance appeared to increase between 1994 and 1998 and then leveled off or declined while the median length increased, suggesting that the strong cohorts of the mid-1980s continued to disperse upstream during the non-sampled years of 1995–1997 but then upstream dispersal declined. This would be consistent with the transition results previously described. The increase in median length in the upper reach at this time might be explained in part by the growth of fish prior to dispersal to the upper reach.

Years 2003–2005. — In 2003 there was a large group of young fish captured from the lower reach (310–429 mm TL), much like in 1991 (Figure 22). This group made up 65% of the lower-reach subpopulation. Many of these were 370–419 mm long and, based on size, were probably age-5 (i.e., the 1998 year class). Or, this group was made up of more than one year-class, with overlapping lengths (i.e., 1997, 1998 and 1999 year classes), as was evidently the case in 1991. However, no scale aging was done to determine cohort overlap. There were very few fish younger than these in the 2003 and 2004 samples. By 2005 many of these were > 500 mm TL. Also in 2005, some fish 330–399 mm TL had appeared and, based on size, were probably age-5 (2000 year class). Individuals ≥ 500 mm TL made up

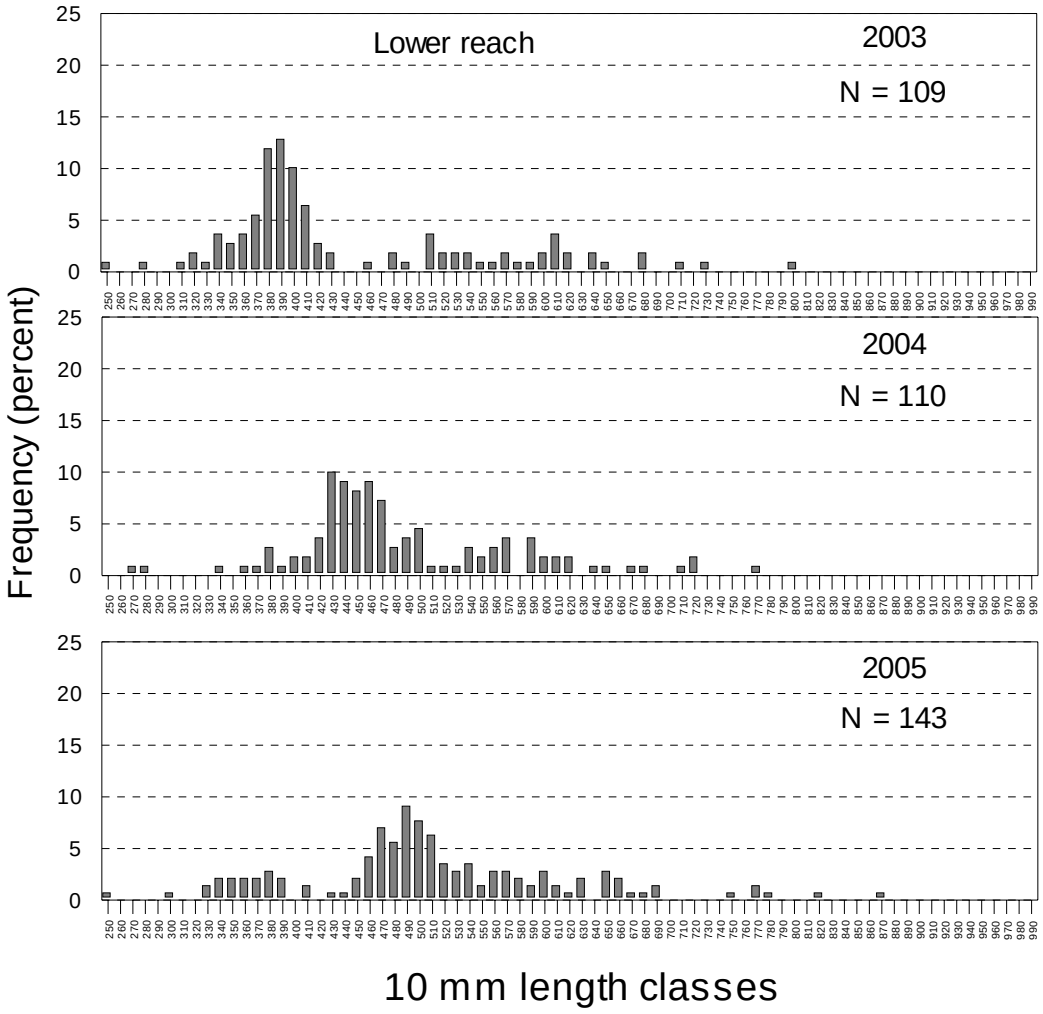

Figure 22. Length frequencies of Colorado pikeminnow captured in the lower Colorado River study reach, 2003–2005.

29% of the 2003 lower-reach sample and 35% of the 2004 sample. By 2005, many individuals of the strong cohort(s) had grown and fish ≥ 500 mm TL made up 53% of the sample. Also, there were more large adults captured in the lower reach during 2003–2005 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, 5–12%.

In the upper reach, there were few young adults captured in 2003: only 4% of the sample was < 550 mm and none were < 500 mm long (Figure 23). Hence, evidence of recent recruitment or dispersal to the upper reach was minimal. In 2004, 7% of the sample was < 550 mm long, and half of these were < 500 mm TL. These may have represented some of

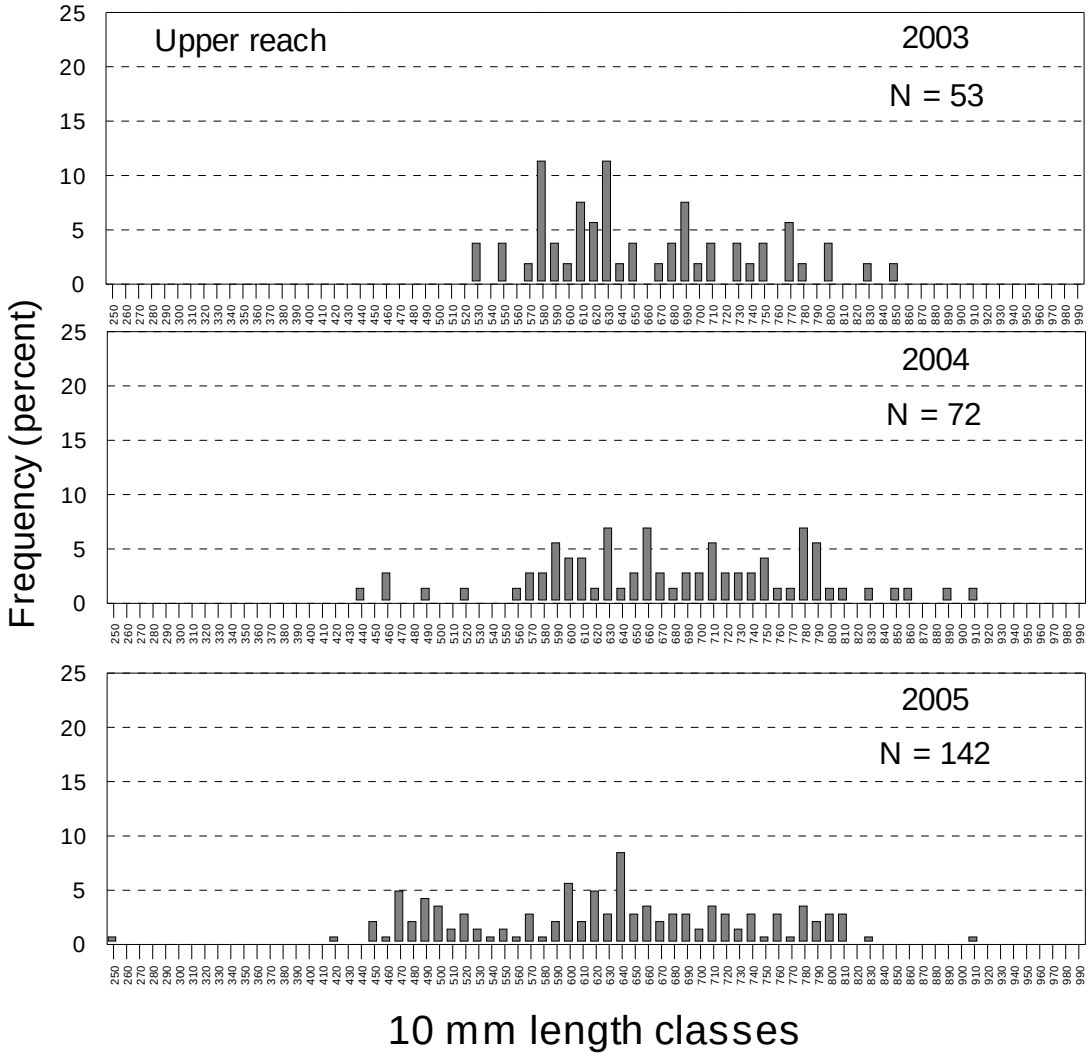

Figure 23. Length frequencies of Colorado pikeminnow captured in the upper Colorado River study reach, 2003–2005.

the first migrants dispersing upstream from the large group of young fish observed in the lower reach in 2003. By 2005, fish < 550 mm TL comprised 25% of the upper reach sample.

The mean and median lengths of upper-reach fish in 2003 (mean: 664; median: 633) were higher than in 2000, and by 2004, were considerably higher (mean: 697; median: 693), continuing the trend seen in 1998–2000 (Figure 21). Again, individuals of the pulse of fish first observed in the early 1990s continued to grow and were now large adults. This, coupled with low numbers of young individuals immigrating from the lower reach would account for increased average lengths. However, this trend was reversed in 2005 when substantial

numbers of sub-adults and young adults appeared again in the upper reach (presumably the 1998 year class) causing the mean and median lengths to decline. The percentages of relatively large individuals (> 650 mm TL) within the upper-reach adult sub-population were similar during the first two sampling periods (1991–1994: 25–35%; 1998–2000: 24–36%), but markedly increased during the recent 2003–2005 period (47–66%), further illustrating the continued effect that growth by the relatively large year-classes produced in 1985–1987 had on the upper-reach adult population. The percentage of adults captured that were very large and old (> 800 mm TL) varied substantially among years: 0–14% during 1991–1994, 3–5% during 1998–2000, and 8–10% during 2003–2005. Curiously, the greatest variability occurred in consecutive years: 14% in 1991, 0% in 1992, and 10% in 1993.

The effect of the new strong cohort(s) on the overall population was most evident when lengths of all fish captured from both reaches were pooled (Figure 24). In 2003, fish 310–439 mm TL were 44% of fish captured. In 2004, fish presumably from the same cohort(s), then 360–499 mm TL, made up 39% of fish captured. By 2005, the length range of this group had become more difficult to distinguish, but appeared to be 410–549 mm TL (see Figure 24). Fish within this length range made up 41% of all captured fish.

Relative Year-class Strength

The appearance and annual relative abundance of age-5 Colorado pikeminnow in the lower reach indicated there may have only been two strong year-classes with origins between 1985 and 2000. As noted above, capture rates and length frequencies provided evidence of a strong pulse of young fish in the lower reach during 1991–1992. Scale aging indicated there was an especially strong year-class produced in 1986, but the year classes of 1985 and 1987 also contributed to this group. The 1988 year class, however, appeared to be very weak based on the relative rarity of age-5 fish in 1993. By 1994, young fish again appeared in the lower reach whose lengths suggested ages 5 and 4. These were not particularly abundant suggesting 1989 and 1990 year-classes were relatively weak, but nonetheless stronger than that of 1988 (Table 6).

After a three-year hiatus, it was difficult to identify year-classes from the 1998, lower-reach, length-frequency histogram. There was, however, a distinct group of fish with

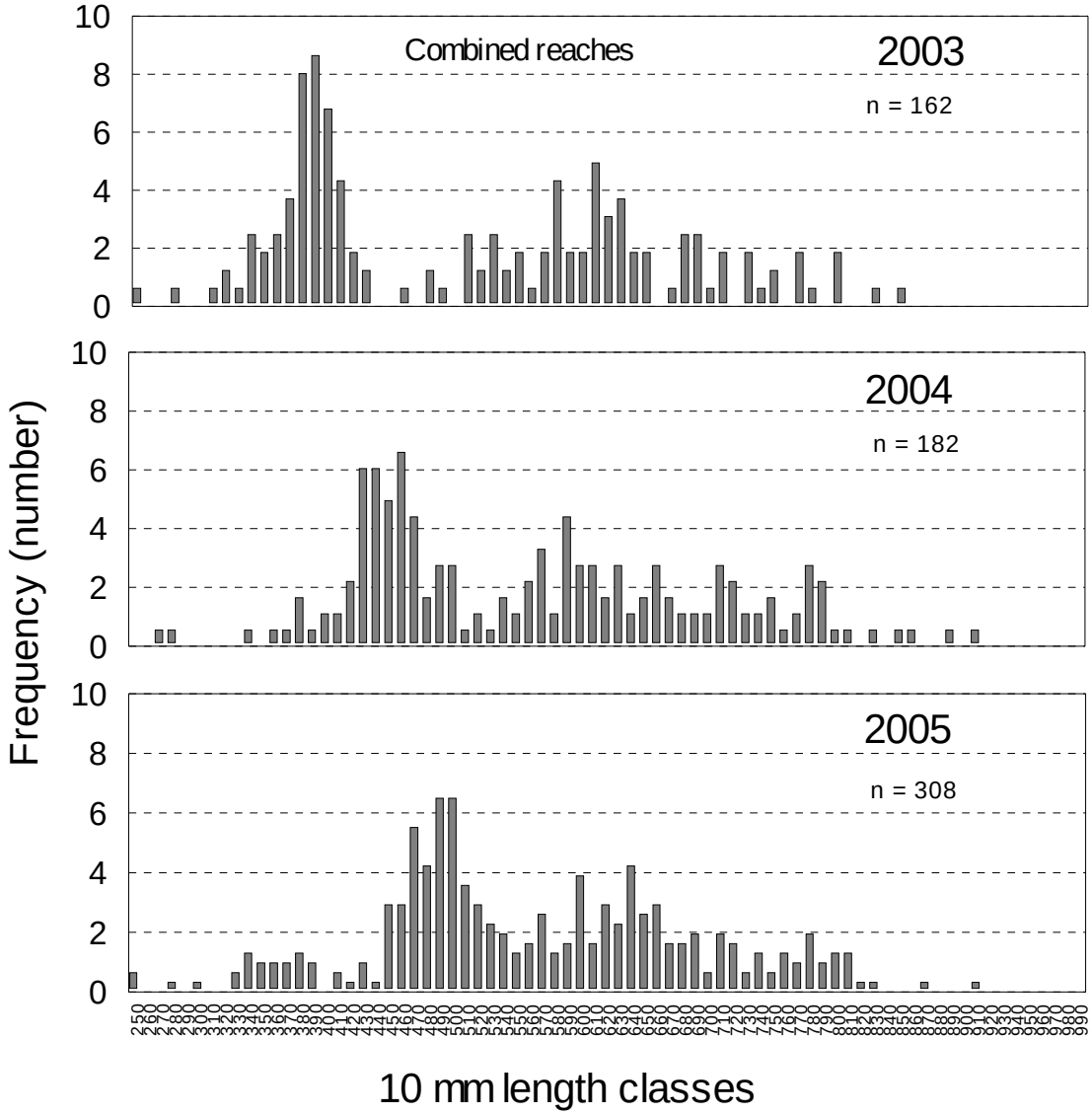

Figure 24. Length frequency of Colorado pikeminnow captured in the lower and upper Colorado River study reaches (data combined), 2003–2005.

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. After this gap there was a continuous block of fish ranging in length from 330 to 510 mm TL. There were no major spikes or gaps

Table 6. Qualitative estimates of Colorado pikeminnow year-class strength based on length-frequency histograms from the Colorado River lower-reach study area, 1991–1994, 1998–2000, and 2003–2005.

Year	Low	Moderate	Strong	Year	Low	Moderate	Strong
1985		x		1993		x	
1986			x	1994	x		
1987		x		1995	x		
1988	x			1996	x		
1989	x			1997	x		
1990	x			1998			x
1991		x		1999		x	
1992		x		2000		x	

within this group suggesting a series of weak-to-moderately strong year-classes from perhaps 1989 through 1993. The 1999 histogram indicated a higher abundance of fish with ages estimated at 6–8 years, or the 1991, 1992 and 1993 year classes, and lends some support to the above observation that 1989 and 1990 may have produced relatively weak year-classes. There were also a few fish captured in 1999 that appeared to be age 4 and/or age 5; in either case, their low numbers in the captured sample suggests that 1994 was also a relatively weak year-class. In 2000, the almost complete absence of fish captured with lengths indicating ages 4 and 5 suggests that 1995 and 1996 were very weak year-classes. After 2000, there was a two-year hiatus in sampling.

When sampling recommenced in 2003, a large pulse of what appeared to be age-5 fish was evident in the lower reach. The smaller of these may have been age-4. However, we assumed most to be age-5 and their abundance suggested that 1998 was a strong year-class. There was a very low number of fish 436–509 mm long, suggesting that ages 6-, 7- and 8-year fish represented weak year-classes (1997, 1996 and 1995). The 2004 histogram indicated a much smaller number of age-5 fish; hence, the 1999 year-class was of low to moderate strength. Finally, in 2005 there appeared a new, distinct length-class that corresponded to sizes expected of age-5 fish, i.e., the 2000 year class. Their relative abundance in the sample suggested a year class of moderate strength.

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

A fish year-class, strong at age-5, or when later recruiting to the adult population, is so 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. Understanding how environmental factors affect production of young and survival of juveniles, and ultimately recruitment level, is prerequisite to devising management strategies aimed at increasing the size of small populations. As a first step, it would be useful to know at what stage a cohort exhibits an increase or decrease in relative abundance. Annual sampling of drifting larvae during the reproductive period of Colorado pikeminnow might allow identification of years of high production of young; however, in the mainstem Colorado River, such sampling has been limited. Seining age-0 fish from backwaters during fall (September-October), when young are 2–4 months old, was systematically conducted annually for 19 years (1982–2000) as part of the ISMP. Catch rates from this fall young-of-the-year (YOY) dataset provide the only available index of age-0 relative abundance against which the strength of an age-5 cohort can later be compared.

The strong pulse of juveniles 310–410 mm TL (ages 4–6 years) first noted in the lower reach in 1991 corresponded to year-classes that previously exhibited relatively high abundance as larvae or as fall YOY. The catch rate of Colorado pikeminnow larvae was highest in 1986 during a 1986–1994 annual dip-net sampling program of upper-reach shorelines and backwaters. Upper-reach, seining catch rates of fall YOY in backwaters during the same period were also highest in 1986, followed by 1987 (Osmundson and Burnham 1998). Perhaps more relevant are the results of the river-wide ISMP fall sampling of YOY mentioned above, as summarized by McAda et al. (1994) and McAda (unpublished data). These results indicate that both 1986 and 1985 were years of relatively high catch rates of 2–4-month-old Colorado pikeminnow (Figure 25).

This linkage between high catch rates of young fish in their first year and high catch rates of juveniles 4–6 years later suggests that factors that limit numbers of age-5 juveniles may occur in the first year of life, and that relative abundance of age-0 fish may be a good predictor of later abundance of the same year-class at age-5 or when later recruiting to the

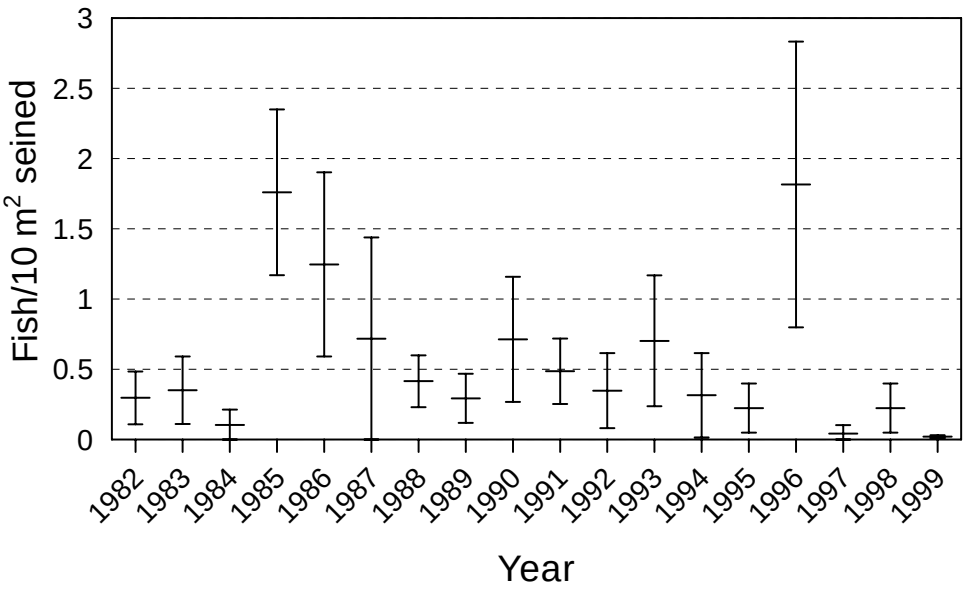

Figure 25. Interagency Standardized Monitoring Program (ISMP) catch-per-unit-effort of young-of-the-year Colorado pikeminnow in the Colorado River, 1982–1999 (Data from McAda et al. 1994 and C. McAda, unpublished data).

adult population. However, more recent data presented here do not support this earlier observation. The results from ISMP indicate that after 1985–1986, the next year with exceptionally high catch rates of fall YOY was 1996. Based on the annual length-frequency histograms of juveniles and adults captured during this study, the 1996 year-class did not later result in high numbers of age-5 juveniles. In fact, 1996 was identified above (previous section) as a year-class with one of the lowest levels of abundance at age-5 years (Table 6).

Body Condition

A pattern of declining body condition with increased fish length in the lower reach and increasing body condition with increased fish length in the upper reach was earlier reported for fish captured during the 1991–1994 period (Osmundson et al. 1998). Additionally, a river-wide decline in Colorado pikeminnow body condition between the 1991–1994 and 1998–2000 sampling efforts was noted by Osmundson (2002). Here the 2003–2005 data is examined to see if the aforementioned pattern and earlier river-wide decline was still evident.

Differences among length classes. — Mean relative body condition (K_n) of lower-reach fish during 1998–2000 decreased with increased fish length as it had during 1991–1994. This phenomenon was again evident in 2003-2005: mean K_n differed significantly between 300–399 mm and 400–499 mm length-classes, between 400–499 mm and 500–599 mm length-classes, and between 500–599 mm and 600–699 mm length-classes (Figure 26-bottom).

In the upper reach, body condition increased with fish size in all three sampling periods (Figure 26-top). Mean K_n was not always significantly different among length-classes but upward trends were generally similar. During 1991–1994 and 2003–2005, mean K_n appeared to decline after fish reached 800 mm TL; however, differences between fish 700–799 mm TL and fish 800–899 long were not 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 26-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. 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 26-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.

Differences among years. — The above analyses and accompanying graphs focus on differences in K_n among length-classes within sampling periods (within reaches), and also within length-classes among sampling periods (within reaches). To simplify monitoring relative body condition through time, the mean K_n of one length class 500–599 was used as an index for making among-year comparisons.

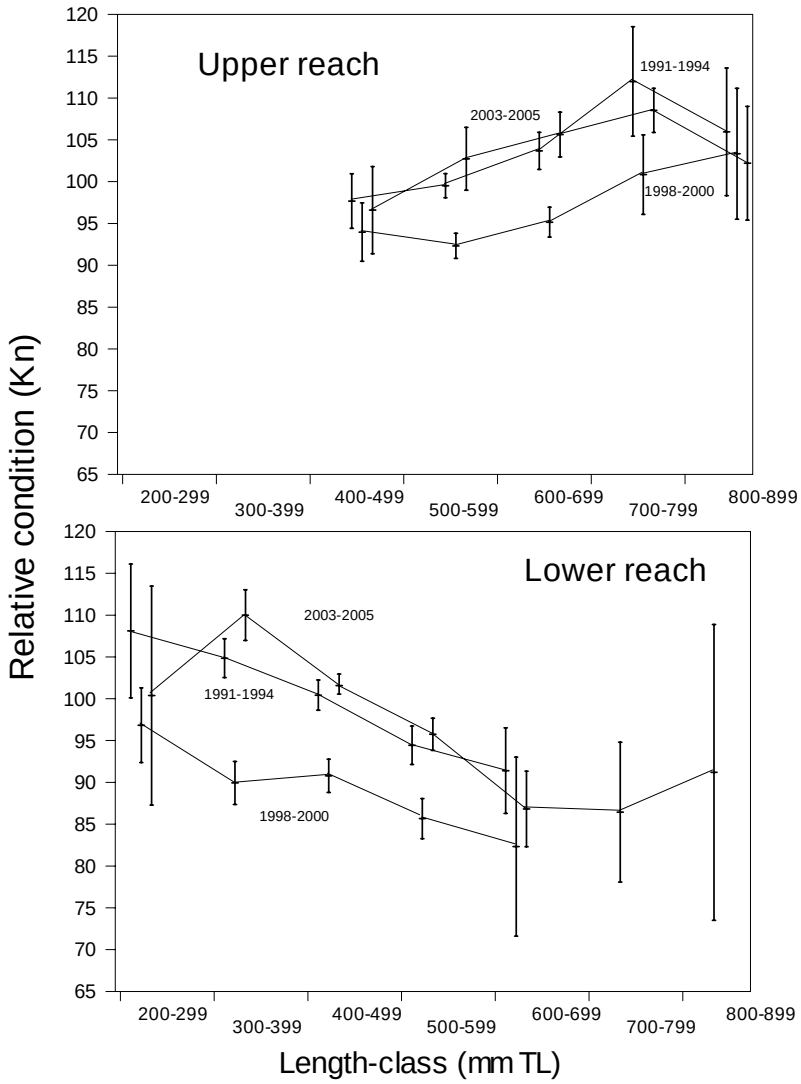

Figure 26. Mean relative body condition (K_n) of Colorado pikeminnow in the upper and lower reaches of the Colorado River study area during three sampling periods, 1991–1994, 1998–2000, and 2003–2005. Means are for seven 100-mm length classes. Data from all years within each multi-year period were pooled before calculating means. Upper and lower bars represent 95% confidence intervals.

In the lower reach, mean K_n of fish 500–599 mm TL was similar among years within the first sampling period (Figure 27-bottom). However, mean K_n then apparently declined sometime during the subsequent three non-sampling years. When fish were again sampled in 1998, their condition was the lowest of any sampled year. During the next two years, mean K_n progressively increased; by 2000 it was significantly higher than in 1998. This upward

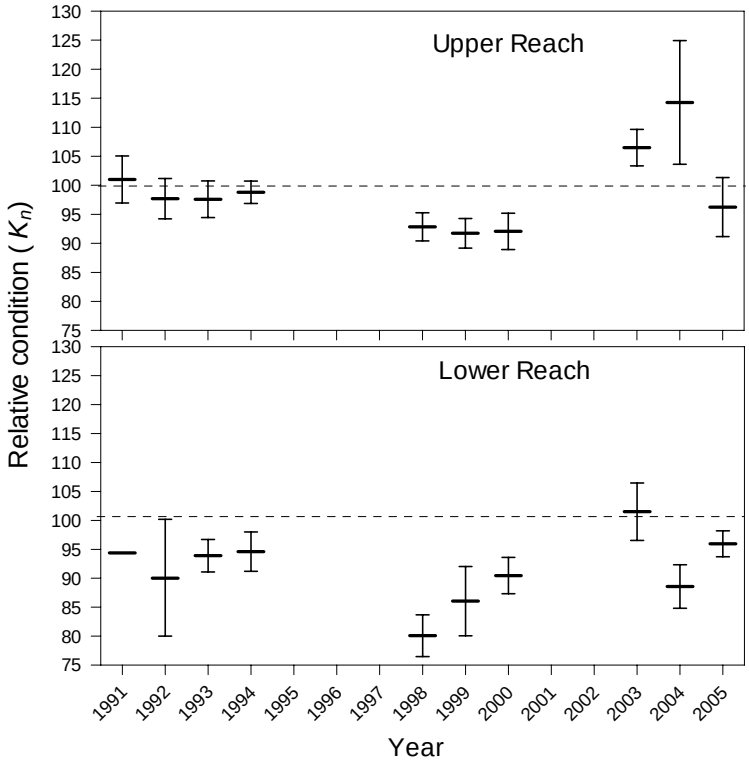

Figure 27. Mean relative body condition (K_n) of Colorado pikeminnow 500–599 mm TL by year in the upper and lower reaches of the Colorado River study area. Dashed horizontal lines at K_n = 100 represent the average relative body condition for the population calculated from all fish captured during 1991-1994.

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 significantly declined again by 2004. Finally, in 2005, it had again significantly increased and was similar to levels observed during 1991–1994.

In the upper reach, mean K_n of fish 500–599 mm TL was also similar among the first four years of sampling (Figure 27-top). Between 1994 and 1998 it significantly declined and remained reduced 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 in the 15-yr period. By 2005, it was significantly lower than in 2003 but was similar to 1992–1994 levels.

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 in the lower reach while it may have increased (not significantly) in the upper reach. Finally, mean K_n significantly increased between 2004 and 2005 in the lower reach while it significantly decreased in the upper reach.

Relations with abundance -- No relationship was found ($r^2 = 0.15$; $P = 0.27$) between our annual upper-reach abundance point estimates of fish $\geq$ 450 mm TL and the annual mean K_n of fish 500–599 mm TL from the upper reach. Considering the variation in annual abundance point estimates, another option was to simply look for a positive or negative slope in mean K_n over time given that we earlier demonstrated a significant positive slope in annual abundance estimates. There was no slope for either upper-reach fish ($r^2 = 0.06$; $P = 0.48$) or lower-reach fish 500–599 m TL ($r^2 = 0.06$; $P = 0.54$), indicating neither an upward or downward trend in mean relative body condition over the study period.

Finally, we compared mean K_n of Colorado pikeminnow in 1992 with those in 2005, given that the combined-reach, abundance, point estimates of fish $\geq$ 500 mm TL increased from 342 to 663. Although the confidence intervals in Figure 27 tell the story, a two-sample *t*-test confirmed that mean K_n of fish 500–599 mm TL in the upper reach in 2005 (96.3) was not significantly different from the 1992 mean of 97.7 ($P = 0.63$).

Comparing annual means of all fish caught (all sizes) in the upper reach also indicated no significant difference in body condition between the two years (1992 mean $K_n = 100.8$; 2005 mean $K_n = 99.6$; $P = 0.44$). In the lower reach, small sample size ($n = 4$) of fish 500–599 mm TL in 1992 precluded using statistical tests to make comparisons; however, for fish 400–499 mm long, mean K_n in 2005 (99.4) was significantly lower ($P = 0.01$) than in 1992 (104.3). Despite this, it would be difficult to characterize the 2005 fish as being in low or poor condition given that mean K_n was still very close to the overall population mean (100.0)

calculated from fish of all lengths from both reaches for years 1991–1994. When mean K_n of all fish caught in the lower reach was compared between years, there was also a significant reduction (1992 mean K_n = 101.6; 2005 mean K_n = 96.4; P = 0.02). This difference can be attributed in part to the much greater proportion of relatively large fish (> 600 mm TL) in the 2005 sample (18%) compared to the 1992 sample (6%), which typically have low condition in the lower reach (see Figure 26).

Movements Into and Out of the Green River System

Although the Colorado River study area was closed to emigration at its upstream end (blocked by the Price-Stubb Diversion Dam), and movement up the Gunnison River was monitored at the Redlands fish ladder and trap (rk 5), it was open to un-monitored immigration and emigration downstream at the Green River confluence. 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) has been surmised (Gilpin 1993) but, until now, undocumented. Although the two systems are treated as separate populations for 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.

Some insight into the frequency of inter-system movements can be gleaned from capture-recapture data collected throughout the upper basin. Although some PIT tags were used in 1990, widespread use did not begin until the following year, 1991. Between 1990 and 2005, there was a total of 10,519 captures reported in the upper-basin (including recaptures) of Colorado pikeminnow that were PIT-tagged at the time of capture or previously (Table 7). These included 2,839 captures (1,546 different fish) in the Colorado River system and 7,680 captures (5,524 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 2005, there was a total of 2,117 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): 586 individuals first captured and tagged in the Colorado system and

Table 7. Total number of Colorado pikeminnow captures in upper basin rivers since use of PIT tags began, 1990-2005. Values do not represent number of different fish captured, rather the number of captures, including recaptures of the same fish. 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 (rk 53.0).

Year	CO[1]	GU[2]	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	**23**
1991	118	3	80	22	66	0	0	0	0	**289**
1992	132	4	123	19	53	0	0	0	0	**331**
1993	209	11	113	71	42	7	0	0	0	**453**
1994	208	41	192	34	19	0	0	0	0	**494**
1995	115	20	429	38	21	0	1	0	3	**627**
1996	120	16	288	42	42	2	6	0	0	**516**
1997	132	4	307	59	23	3	11	0	0	**539**
1998	357	36	479	43	52	3	1	6	0	**977**
1999	264	15	344	71	61	24	2	0	0	**781**
2000	194	11	864	317	140	23	0	0	0	**1,549**
2001	39	3	952	238	236	0	0	0	0	**1,468**
2002	0	7	505	184	49	0	0	0	0	**745**
2003	185	7	388	120	63	0	0	0	0	**763**
2004	192	10	143	0	72	0	0	0	0	**417**
2005	357	6	155	0	29	0	0	0	0	**547**
Total	**2,645**	**194**	**5,362**	**1,258**	**968**	**62**	**21**	**6**	**3**	**10,519**

[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

1,531 individuals similarly captured in the Green River system. Hence, 38% of the different Colorado-River-captured fish were recaptured at least once and 28% of the Green-River-captured fish were recaptured.

During 1990–2005, there were 33 documented inter-system movements (Appendix Table VI). Seven of these capture-recapture events occurred only one year apart; another eight 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 not all. At least 17 fish were ≥ 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. Seven fish moved over 644 km (400 miles) 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 1,588 km (987 miles) in a three-year period. Thirteen of 17 (76%) fish that moved from the Colorado system were tagged and last captured in the Colorado River within 113 km (70 miles) of the confluence, whereas only four of 13 (25%) fish that moved out of the Green River were tagged and last captured within 113 km of the confluence. Ten of the 30 different fish that made inter-system movements first did so from locations at least 161 km (100 miles) 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 (71%) 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; three in the Yampa River; one in the White River. One fish that moved from the Green River was next caught in the Gunnison River; all others were caught in the mainstem Colorado River.

Of the 2,117 unique, upper-basin Colorado pikeminnow that were captured two or more times, 1.42% had made at least one inter-system movement. Seventeen individuals captured in the Colorado River system moved to the Green River system and 13 fish captured in the Green River system moved to the Colorado River system. Three of these fish moved to the other system but later returned; hence, six of the 33 inter-system movements were made by three fish. Two 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, slightly more fish moved from the Colorado River system to the Green River system than those that moved in the opposite direction (17 fish moved to the Green versus 13 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 1,546 unique Colorado pikeminnow captured in the Colorado River system, 0.84% had previously

been tagged in the Green River system, and of the 5,524 captured in the Green River system, 0.31% had previously been tagged in the Colorado River system. The higher percentage of immigrants in the Colorado River system than in the Green River system should not be surprising given that the number of individuals tagged in the Green River system that could move and be detected in the Colorado system was much higher than the number tagged in the Colorado River system. Conclusions regarding net movement are difficult to make from these data because comparisons do not take into account unknown differences in sampling effort 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.).

A higher percentage of Colorado-River-tagged fish emigrated to the Green River system than Green-River-tagged fish emigrated to the Colorado River; however, from a numerical standpoint, Colorado River emigration may have been roughly balanced by immigration. Of 586 fish initially tagged in the Colorado River system and recaptured at least once, 2.9% were recaptured in the Green River system, and of 1,531 fish initially tagged in the Green River system and recaptured at least once, 0.9% were recaptured in the Colorado River system. At least two 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 2.6% of Colorado-River-tagged fish emigrated to the Green River system compared to an estimated 0.8% of Green-River-tagged fish that emigrated to the Colorado River system. Because the long-term recapture rate has been higher in the Colorado River system than in the Green River system (38% in the Colorado River system; 28% in the Green River system), 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. Hence, the above statistics may underestimate the 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 to the Colorado River population from 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 15 fish that we know emigrated (and presumably

did not return) and the 12 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.

Captures of Stocked Colorado Pikeminnow

Some hatchery-reared Colorado pikeminnow stocked in the Gunnison and Colorado rivers by the FWS and CDOW in 2003 and 2004 (Table 8) were captured during the sampling efforts for this study in both 2004 and 2005. Only 12 fish were stocked in spring 2003 (April) that could have been captured during spring 2003 sampling; none of these were. Others stocked that year were stocked in October and November, after the 2003 spring sampling. None of these were later captured in 2004 or 2005. Two hatchery-reared fish were captured in 2004; these had been stocked May 18 in 2004 near Rifle, Colorado (RM 240.7). One had traveled 168 miles downstream (to RM 72.7) in nine days, the other, 184 miles (296 km) downstream (to RM 57.1) in eight days. Another 22 hatchery-reared Colorado pikeminnow were captured from Grand Valley canals in 2004 (Nov. 17–19) during unrelated fish salvage efforts when canals were drained in late fall. All had been stocked at Rifle: five stocked on May 18; the remainder, on September 15. All were returned to the river downstream of the diversions.

In 2005, 45 stocked fish were captured in the study area, five of which were captured twice. All had been stocked in 2004: 31 from the Gunnison River stocking; nine from the May 18 Colorado River stocking. None was from the September 15 stocking, and none was from the group salvaged from canals the previous fall. Nine of the 45 fish were captured in the Grand Valley and 36 were captured in the lower reach. Five of the Grand-Valley-captured-fish were from the Gunnison River stocking and all were caught downstream of the Gunnison River confluence. Only one stocked fish was caught in the Colorado River upstream of the Gunnison River confluence and it had been stocked upstream in the Colorado River. Of the 36 fish caught in the lower reach, 23 were caught downstream of Moab, Utah (RM 64), including five within 8 km (5 miles) of the Green River confluence.

All 45 stocked fish captured in 2005 had been in the river approximately one year and their mean length at capture was 280 mm (range: 224–320 mm). The mean growth

Table 8. Colorado pikeminnow stocking information for the Colorado and Gunnison rivers, 2003 and 2004. Abbreviations: RM = river mile; FWS = U.S. Fish and Wildlife Service; CDOW = Colorado Division of 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	CDOW	Colorado	240.7	1,164	184	134–292
Jun 01	CDOW	Gunnison	57.0	1,200	217	142–270
Sep 15	CDOW	Colorado	240.7	651	204	150–235
Total				**3,015**		

increment while in the river was 64 mm (range: 31–114 mm). Though stocked in 2004, these fish were part of the 2002 year-class and were therefore age-3 when captured. Their size corresponded to wild fish between age-3 and age-4 years. Colorado pikeminnow of this size were rare in the wild population in 2005. Hence, stocked fish dominated what would have been the 2001 and 2002 year-classes, based on the length-frequency histogram of captured fish (Figure 28). Model M_o of Program CAPTURE, run separately for these fish, provided a combined-reach estimate of 190 individuals (95% CI = 100–426) inhabiting the study area during the 2005 spring sampling period (164 in the lower reach; 25 in the upper reach), or approximately 3.7% of the number stocked. Model M_o + length changed the result only slightly: 192 individuals (95% CI = 100–440). These estimates are probably low because of individual heterogeneity not accounted for with the M_o model; however, Pledger mixture models were not useful because of the low detection probabilities and low number of capture occasions. In contrast, wild fish 280 mm TL in the lower reach had an estimated annual survival rate of 67% in 2005. 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 turned up none (USFWS unpublished data). Four stocked fish were later

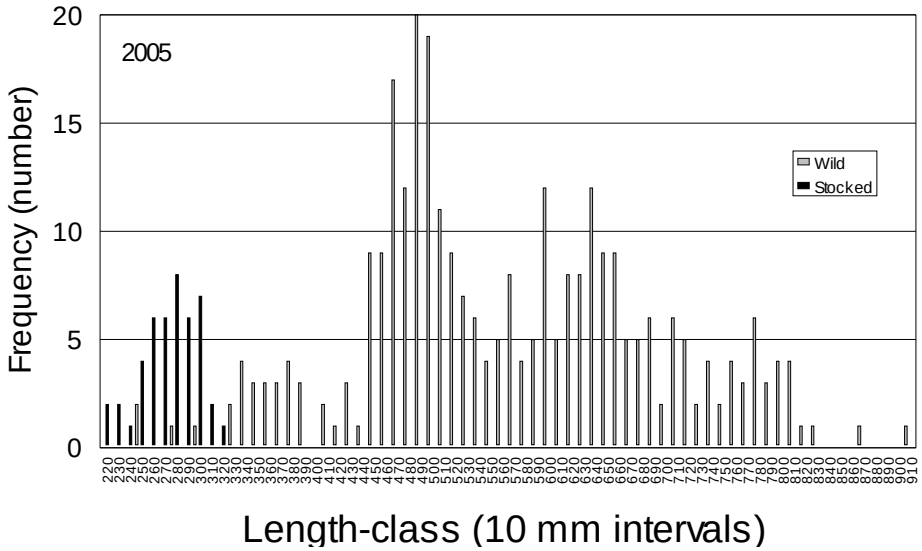

Figure 28. Length frequencies of stocked and wild Colorado pikeminnow captured from the whole Colorado River study area in 2005.

captured in 2008 in the Colorado River study area based on an initial scan of recent capture records (USFWS unpublished data).

DISCUSSION

Abundance and Survival Estimates

Abundance estimates generated with the Huggins estimator were generally higher than those previously reported and generated from Program CAPTURE (Table 9). The mean difference between annual estimates was 14% and can be attributed to length affecting capture probability. The Huggins estimator used length as a covariate in the estimation process and thus better accounts for individual heterogeneity whereas CAPTURE did not incorporate information from length to model individual differences.

Table 9. Estimates of Colorado pikeminnow population size in the Colorado River study area (combined reaches) for fish ≥ 450 mm long using two estimators: CAPTURE($M_{0+}M_t$) and MARK(Huggins). The 1991–1994 and 1998–2000 CAPTURE estimates are from Osmundson (2002); the 2003–2005 estimates are from annual reports. The CAPTURE estimate for 2000 differs from that presented in the 2002 report (719) because it was later found that one recapture had been counted twice.

Year	Population Size CAPTURE/$M_{0+}M_t$	Population Size MARK/Huggins	Percent change
1992	382	440	+15.2
1993	476	705	+48.1
1994	652	687	+5.4
1998	583	583	0.0
1999	512	589	+15.0
2000	690	773	+12.0
2003	784	661	–15.7
2004	481	688	+43.0
2005	870	889	+2.2
Mean			+14.0

Combined-reach abundance estimates of Colorado pikeminnow ≥ 450 mm TL (Recovery Goal adult length criterion) exhibited a positive and significant slope during the 13-year study period (1992–2005). For individuals ≥ 450 mm TL, the most recent (2005) estimate suggests a population size of 889 (CI = 746–1,075).

The pattern of capture probability as a function of fish length in the two study reaches of the Colorado River system was notably different from that in the Green River system. In the Green River study area, distributions of capture probabilities were bell-shaped with probabilities being equally low for the smallest and largest fish, and capture probabilities were highest for fish 500–600 mm long (Bestgen et al. 2007). In the Colorado River, probabilities of capturing the largest individuals were greater than the probabilities of capturing individuals less than 500 mm TL and the highest capture probability was for fish about 750 mm TL.

Survival rate as a function of fish length followed a similar pattern to that found in the Green River in 2000–2003 in that survival increased with fish length up to a length of about 600 mm and then declined with larger size. However, there was one notable difference: survival rate of fish ≥ 800 mm TL was essentially zero in the Green River system (Bestgen et al. 2007) whereas in the Colorado River system, survival rate in the upper reach was 80% for fish 850 mm TL and declined to 67% for fish 960 mm long (965 mm was the largest fish captured during the study). Survival rate for individuals ≥ 500 mm TL exhibited an apparent decline during the overall study period, from 88% in the first period to 80% during the latest period, but overlapping confidence intervals prevented us from concluding this decline was real. Bestgen et al. (2007) reported survival rate in 2000–2003 as 65% in the Green River system but included all sizes of fish in the analysis; hence, our estimates for fish ≥ 500 mm TL could not be directly compared.

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, with a summed net gain of 332 individuals ≥ 450 mm TL. Although these estimates are imprecise, and gains and losses for some years during the 14-year period could not be estimated, the requirement of the Recovery Goals that mean annual recruitment equal or exceed mean annual adult mortality appears to have been met. These results also support the notion that the adult population increased in abundance during the study period.

To meet the Recovery Goal requirement that the adult population not decline significantly over a specified monitoring period, we found that the abundance estimate of the last year of such a period would have to be 30% less than that of the first year to be significantly different at $\alpha = 0.05$, assuming a mean CV similar to that obtained during the most recent three-year sampling period (15%). Hence, for a five-year monitoring period, a decline would have to be substantial for it to be statistically significant. With the CV we obtained in 2005 (9.4%), abundance would have to decline by 20% to be significant ($\alpha = 0.05$). This was our most precise estimate (lowest CV) and required five passes, including supplemental post-spawning captures. It probably represents the best sampling effort we can hope to achieve. Assuming a CV of 15%, a 30% decline could occur fairly rapidly if there

was a complete lack of recruitment. At a survival rate of 85%, an adult population of 1,000 could decline to 723 in two years (28% decline) and to 614 in three years (39% decline).

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 7 and Table 4). Upstream movements of this first pulse of young fish had evidently almost ceased by 1998 (Psi = 0.0), perhaps indicating the pool of fish inclined to move had become depleted. Additionally, the decline in upper-reach point estimates from 1998 through 2004 was consistent with the zero, low, and negative net upstream probabilities estimated for those years. Finally, a notable increase in upper-reach abundance in 2005 was consistent with the high net upstream transition probability (30%) estimated for the 2004–2005 period. Although all of these increases and decreases in annual abundance point estimates were not statistically significant, they did fit what we might expect given the net transition probabilities.

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. 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 change in direction of net movement in 2003 (no additional downstream movements) coincided with a significant improvement in mean *Kn*. Though speculative, this causal explanation of downstream movements deserves consideration and perhaps future hypothesis testing.

Electrofishing Catch per Effort

Although ISMP sampling reaches provided a good representation of river-wide catch rates, the reliability of electrofishing catch rates as an index to relative abundance of Colorado pikeminnow remains unclear. The mark-recapture estimates indicated a clear upward trend during the period 1992–2005; yet no such trend was evident from electrofishing catch rates during the same period. Population monitoring using catch rates as an index to relative abundance assumes that probability of capture is mostly uniform across years and rates of capture are therefore expected to be proportional to abundance in a consistent manner. In the past, inconsistencies between trends in population estimates and trends in catch rates raised doubt about the accuracy and reliability of the mark-recapture abundance estimates in some years (Osmundson 2002). However, results here indicate high variability in annual capture probability, violating one of the key assumptions of catch-per-effort indices. 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 than catch-rate results for discerning population trends.

In contrast to our results, Bestgen et al. (2007) found good agreement between catch-rate and abundance estimation trends when analyzing Colorado pikeminnow monitoring results from the Green River system. Our findings from the Colorado River are not conclusive because of two confounding issues that we were unable to resolve. One was that the protocol for electrofishing shorelines for this study was somewhat different from that used during ISMP and may have negatively biased mean CPE results. In our study, when an electrofishing boat was accompanied by a trammel-netting boat on a given day, the electrofishing crew was instructed to avoid sampling backwaters so that fish were not scared away prior to arrival of the netting boat. In contrast, during ISMP, electrofishers were

allowed to shock backwaters and this may have allowed them to catch more fish. Hence, the data sets are not entirely comparable. When the 2003-2005 catch rate data from our study were removed from the long-term catch rate data set, a significant upward trend was indicated. Additionally, early ISMP electrofishing utilized VVP (variable voltage pulsator) units to produce pulsed DC. Recent studies, including ours, have used VVP units on some boats and GPP units on others. Difference in capture efficiencies of these two unit types is unknown but could potentially bias early-versus- recent catch rate comparisons.

A second issue was that the probabilities of capture calculated here were based on a combination of electrofishing and trammel-netting captures. Hence, the level of temporal variability in capture probability for electrofishing alone was not measured and thus could have been more or less than that indicated by the combined-gear results. If variability in capture probability for electrofishing was in fact low, then violation of this key assumption may not have been important. However, investigators in the Green River system, who relied almost exclusively on electrofishing for mark-recapture sampling, also found high among-year variability in capture probability (Bestgen et al. 2007), suggesting this may indeed be a serious shortcoming of catch-rate based trend analysis.

Length Frequency

Length-frequencies of captured Colorado pikeminnow were useful in identifying strong and weak year-classes; however, because probability of capture varies with fish size, it should be noted that frequencies of various length-classes from capture data do not necessarily provide an accurate representation of relative abundance of length-classes in the population. This effect poses less of a problem in the upper reach because most fish there are of adult size. In the lower reach, length frequencies are more biased because young (smaller) fish have a lower probability of capture, resulting in an over- representation of larger fish in a sample. To illustrate the overall effect, we applied correction factors to the observed frequencies of each length-class in the samples from 2005, with the correction factor based on the relation between probability of capture and fish size. Although the basic shapes of the histograms were retained, the lower-reach distribution revealed that fish < 480 mm TL were under-represented in the sample and fish > 490 mm TL were over-represented (Figure 29).

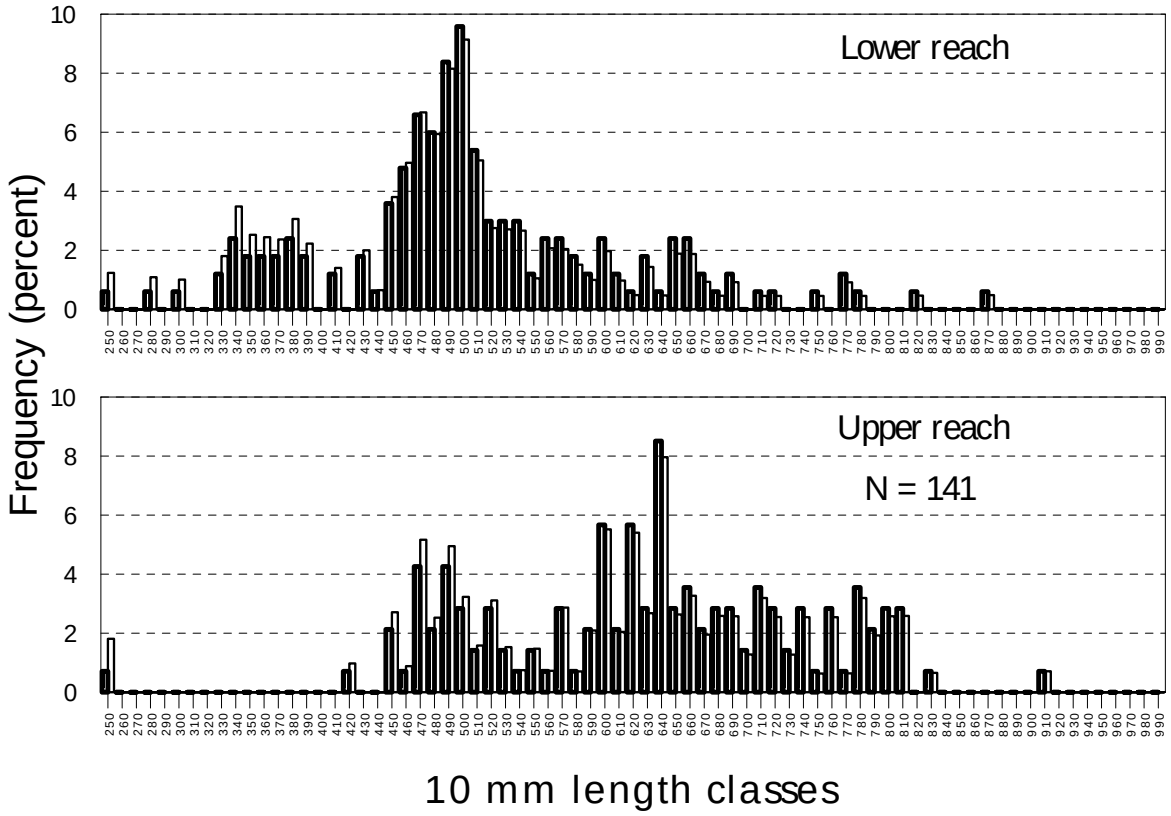

Figure 29. Difference in Colorado pikeminnow length frequencies between the 2005 sample of fish captured from the upper and lower Colorado River study reaches (grey bars) and the estimated actual population when the frequencies of sampled fish were adjusted by length-specific probabilities of capture (black bars). The correction factor applied to the number of captures in each length class was p^*, the probability of capturing a fish one or more times during the 5 passes, derived from the beta estimates from the top model such that $p^* = 1 - (1 - p_1)(1 - p_2)(1 - p_3)(1 - p_4)(1 - p_5)$. Length class labels represent the lower end of a 10-mm group, i.e., one labeled 300 includes fish 300–309 mm TL.

The estimated actual frequency of the smallest fish (250–259 mm TL) was twice that found in the sample. In the upper reach, fish in the captured sample < 590 mm TL were under-represented and fish > 600 mm TL were over-represented. However, the purposes for which we used length frequencies in this study (identification of strong year-classes), should not be affected by these biases.

Relative year-class Strength

Our best estimates of year-class strength based on relative abundance of age-5 fish in ten annual length-frequency distributions suggested there were only two strong year-classes between 1985 and 2000. These two years, along with seven years of moderately strong year-classes, together fueled a significant increase in the adult population. This was despite seven of the 16 years (44%) having weak year-classes. Based on a comparison of 1992 and 2005 combined-reach, abundance, point estimates, the adult population may have doubled in size during the study period, regardless of whether the ≥ 450 mm TL or ≥ 500 mm TL length criterion is used for defining adults.

Although no abundance estimate was available for the lower reach in 1991, the length frequency histogram of that year indicates there were very few individuals ≥ 450 mm TL present and even fewer individuals ≥ 500 mm TL. A rough estimate of lower-reach adults in 1991 can be obtained by applying the 1991 percent composition of these length-classes to the 1992 lower-reach abundance estimate of fish > 250 mm TL. When such an estimate is added to the 1991 upper-reach estimate, about 218 adults are indicated for the river-wide, 1991 population. If true, the number of Colorado pikeminnow ≥ 450 mm TL may have only been about 25% of that estimated for 2005; for those ≥ 500 mm TL, only 28%. Hence, Colorado pikeminnow adults, numbering around 200 in 1991, exhibited a marked increase in abundance during the 14 years of our study despite a 44% rate of weak age-5 year-classes. Strong year-classes of 1986 and 1998 were evidently critical contributors to this population increase. One implication of this is that year-classes leading up to 1985 must have been especially poor for a long period to have allowed the population to drift down to the small number observed in 1991. The extreme scarcity of adults in the lower reach in 1991 might be explained by a long series of prior weak year-classes in combination with dispersal to the upper reach of those few fish that did successfully rear in the lower reach during prior years.

Year-class Strength and Later Recruitment

The apparent loss of the initially strong (based on high fall YOY catch rates) 1996 cohort was unexpected and therefore deserves a closer look. For reasons previously given,

aging fish based on their length is not an exact science. In fact, scale aging, upon which estimates of mean length by age of young fish are based, is not infallible either. For instance, if a given fish lays down an annulus during the first year when it is assumed that it did not (see Hawkins 1992), a scale-aged fish may in fact be a year younger than estimated. If this occurred, the strong year-class identified from scale-aging fish captured in 1991 and 1992 (see Osmundson et al. 1997), should have been the 1987 year-class instead of the reported 1986 year-class, and mean lengths by age would have been underestimated. The ramification of this would be that a pulse of age-4 fish (the 1996 year-class) with a mean length of 376 mm instead of 315 mm should have appeared in the length-frequency histogram of 2000. However, no new pulse of any size appeared that year. Thus, the absence of the initially abundant 1996 year-class cannot be ascribed to a faulty assumption regarding the missing first annulus in scales.

In addition to the apparent disappearance of the initially-strong 1996 year class, the large pulse of what we believed to be age-5 Colorado pikeminnow noted in the lower reach in 2003 (the first like it since 1991) also exhibited no linkage to the relative abundance of its cohort in the estimated year of origin (i.e., catch rate of fall YOY in 1998 was relatively low). This lack of linkage would be difficult to explain by length-based aging being off by one year because catch rates of YOY of the adjacent two year-classes were also very low, i.e., the 1997 catch rate of YOY was lower than in 1998 and the 1999 YOY catch rate was the lowest on record (Figure 25). Hence, if the strong pulse observed in 2003 was the 1996 year-class, as might be expected, these fish would had to have been age-7 rather than the estimated age-5, and the estimates of length-at-age used here would be off by two years. Another approach to this question would be to start off with the assumption that strong cohorts in the year of origin will remain strong cohorts until they recruit to the adult population; growth during the intervening years would be evaluated accordingly without any reliance on scale aging at all. Doing this, we would interpret the strong pulse of young fish first detected in 1991 to consist primarily of 1985 (age-6) and 1986 (age-5) year-classes because these were not only equally abundant but also significantly more abundant in the years of origin than any year-class from 1982 through 1991 (McAda and Kaeding 1989, McAda and Ryel 1999). The majority of the fish captured in the lower reach in 1991 were 310-400 mm TL and lengths of the two age-classes would have therefore overlapped

considerably. If the more recent pulse of young fish, mostly 340-420 mm TL, first detected in 2003 was in fact the 1996 year-class, they would have been age-7. For fish of the 1991 and 2003 pulses to have such similar lengths, growth of the 1985 and 1986 year-classes would had to have been rapid whereas growth of the 1996 year-class would had to have been very slow. If this occurred, it must have happened after the initial year of growth. The mean of mean lengths of fall YOY from ISMP collections (1982-1996; n = 15 years) was 35.5 mm (from McAda and Ryel 1999), and the mean lengths for 1985 and 1986, both 27.9 mm, were therefore less than average. Mean length in fall 1996, 39.6 mm, was higher than average. After YOY leave backwater habitats at approximately age-1, temperatures of the main channel likely become more relevant to juvenile Colorado pikeminnow growth rate. Estimated annual thermal units for Colorado pikeminnow growth (ATU; after Osmundson et al. 1998) in the main channel summed to 476 thermal units during 1986-1990 and 411 thermal units during 1987-1990 (see Figure 30). This could have resulted in above-average growth, especially for the 1986 year-class. However, the 1996 year-class would have

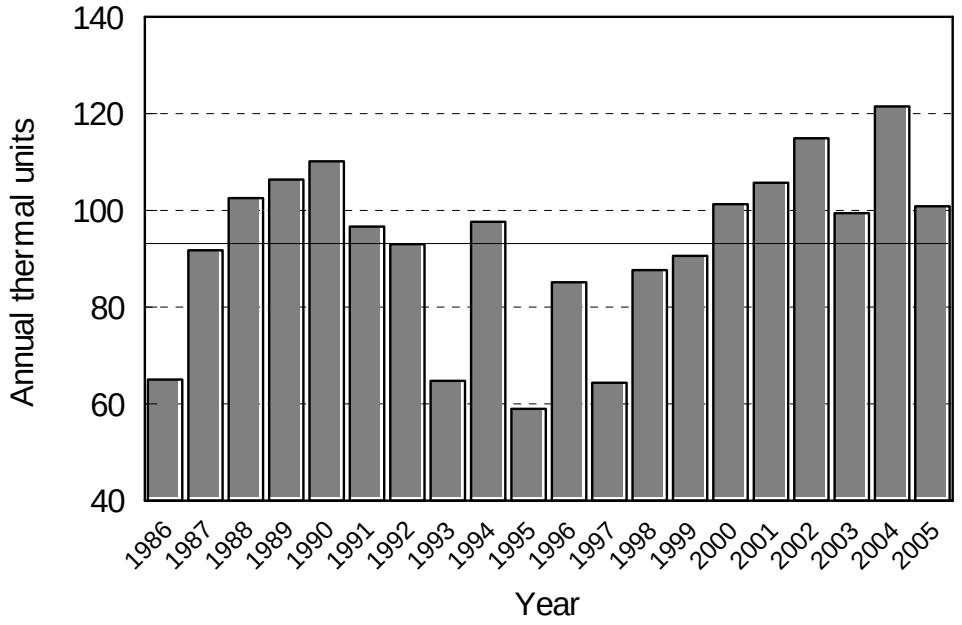

Figure 30. Estimated main-channel annual thermal units (ATU) for Colorado pikeminnow growth at rk 83.7 on the Colorado River, downstream of Moab, Utah, 1986–2005. See Osmundson (1999) for methodology in determining ATU. Horizontal line marks the 20-year mean (92.9 ATU).

experienced a total of 564 thermal units during 1997-2002. Based on fall sizes in the year of origin as well as subsequent main-channel thermal conditions, the 1996 cohort at age-7 should have been notably larger than the 1985 and 1986 cohorts at age-6 and age-5, respectively. Hence, even using this approach, it is difficult to link the 2003 pulse of young fish to the 1996 year-class.

Body Condition and Carrying Capacity

Recovery goals for Colorado pikeminnow state that downlisting may occur (presuming other conditions are met) when the Colorado River population reaches 700 individuals $\geq$ 450 mm TL (USFWS 2002), and is based on the idea that that is the maximum number of healthy adults the system can currently support, i.e., carrying capacity is reached. The idea was originally suggested in a report that outlined the preliminary results of the 1998 population monitoring wherein it was noted that a significant reduction in mean relative body condition coincided with an apparent increase in Colorado pikeminnow abundance (see Osmundson 1999). The reasoning behind the suggested link being that Colorado pikeminnow numbers may have exceeded the supply of available prey, and as a consequence, individuals were losing weight. A spike in use of the Redlands fish ladder at the same time (evidence of emigration) lent support to this idea. With more years of abundance and body condition results now available, we are in a better position to evaluate the 700-adult-carrying-capacity hypothesis.

Mean body condition of lower-reach fish displayed some reduction between the first and last years of study whereas body condition of upper-reach fish did not. The reduction in the lower reach was significant but not large. There, relief exists for Colorado pikeminnow if the system becomes crowded, i.e., they can move to the upper reach. Upper-reach fish are free to similarly move to the lower reach, though evidence suggests comparatively few have done so. However, they can and have moved upstream to the Gunnison River as evidenced by Redlands fish ladder trap data. Although there were relatively high numbers of Colorado pikeminnow using this ladder in 1997 and 1998 (18 and 21), use was low in 2005 (4), the year when estimated abundance was highest.

Osmundson et al. (1998) suggested that scarcity of appropriate-sized prey in the lower reach prompts many adults to move upstream and eventually take up residence in the upper reach (see Osmundson et al. 2002 for discussion of abiotic factors that influence fish assemblage distribution). If the capacity of the lower reach to support adult pikeminnow had been reached, we might expect abundance there to have leveled off within some range, with further additions of adults simply having moved to the upper reach (or perhaps to the Green River) where we would expect abundance to rise until the capacity there was reached. However, lines fitted to the annual point estimates of individuals ≥ 500 mm TL in the lower and upper reaches essentially parallel one another, suggesting adult abundance increased in both reaches at about the same rate (Figure 31). Additionally, we found no relation between abundance and relative body condition in either reach. In the upper reach, there was no difference in mean body condition between fish in 1992 and those in 2005. Given that 2005 was the year with the highest abundance estimate in the upper reach, it would be difficult to make the case that carrying capacity was reached. Similarly, in the lower reach, body condition was highest in 2003, the year with the highest abundance point estimate. Why

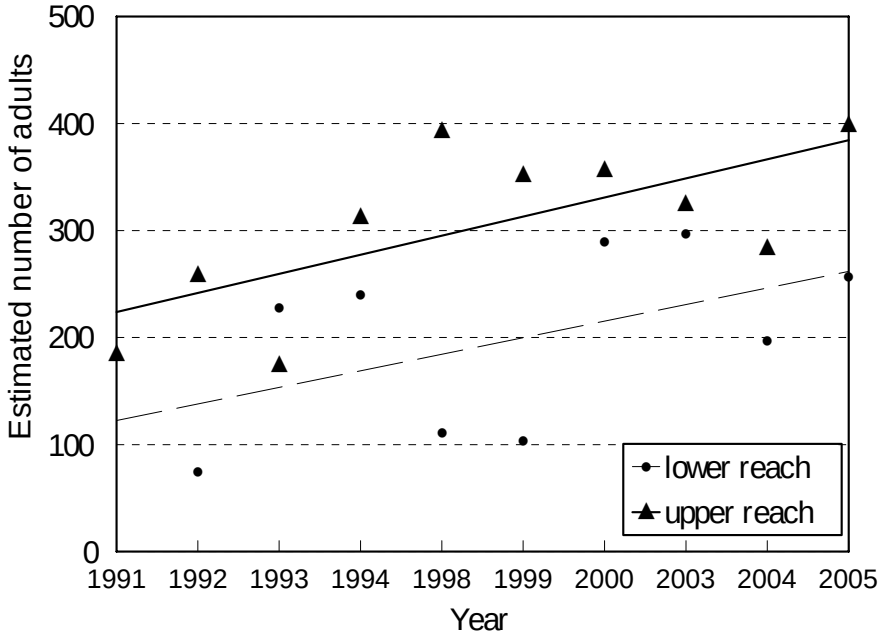

Figure 31. Lines fitted to the annual abundance point estimates for Colorado pikeminnow in the upper and lower reaches of the Colorado River study area.

body condition in the lower reach was at its lowest point in 1998 and in the upper reach during 1998–2000 remains unknown. A temporary river-wide reduction in productivity or forage abundance might provide a causal explanation, but we have no supporting evidence that this occurred.

Assumptions

The robust design multi-state model employed here that produced separate annual 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, with two exceptions 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 the 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, as well 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 33 inter-system movements we documented over a 14-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 15 marked fish that we know emigrated from our study area to the Green River over a 14-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 fish if the individuals that immigrated fell outside of the 400-450 mm length-class. Of the 12 Green River Colorado pikeminnow that we know entered and, we assumed, stayed in the Colorado River, at least nine 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 methods, such as the availability 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.

Inter-system Movement

Evidence presented here of 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. Some possible scenarios would allow gene flow while others might not. We explore some of these scenarios below.

Because a fish is first captured in a given river, it does not necessarily mean that that river is the fish's place of origin. Additionally, young fish may move down river, either as drifting larvae or as swimming YOY, past the confluence and spend their first years in Cataract Canyon or even in Lake Powell. As they develop, upstream dispersal will bring them back to the confluence of the Green and Colorado rivers. If we assume that these young fish have an innate sense to detect their river of origin and have fidelity to it, we might also assume that most proceed up their natal river. Even in such a case, there is likely some percentage of these young fish that, for whatever reason, proceed up the other river, such as Pacific salmon that 'stray' and spawn in a river other than their river or stream of origin (Quinn et al. 1991). It may be several years before an individual senses something is amiss. If these fish have fidelity to their natal river or spawning location when it comes time to spawn, as has been suggested (Tyus 1985), these errant fish may not seek their natal river until they have matured and undertake their first spawning migration. In such a scenario, an individual fish may be caught and tagged in one sub-basin, but finds the natal sub-basin prior to spawning for the first time (no gene flow). However, two of the 14 fish displaying inter-river movements did so relatively late in life (one was > 615 mm TL, the other > 752 mm), suggesting that if this was their first of such movements, they may have been spawning in the 'wrong' river for some time (gene flow). Again assuming strong spawning fidelity to the natal river, it is also possible these errant fish are captured in the 'wrong' river when they are there temporarily to forage, returning to spawn in the 'correct' river some time after being captured (no gene flow). Another possibility is that there is no fidelity to the river of origin and young fish returning upstream move into the Green and Colorado rivers randomly (high gene flow). Similarly, some small percentage of older fish might make exploratory downstream movements, discover the other river, move up it, and for whatever reason take up residence and spawn there (gene flow).

Those few sub-adult or adult fish that make substantial movements downstream one river and upstream 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. 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. So far, this has not occurred, and it may remain unlikely given that sampling is usually conducted prior to the spawning period. 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.

The metapopulation concept probably applies to the groups of Colorado pikeminnow in the two sub-basins. For the most part, the fish of each sub-basin are separated in space, even though a direct connection for migration is continuously provided at the confluence; hence, the populations are not entirely spatially discreet, an assumption of the original metapopulation concept (Levins 1969). However, more recent use of the term and concept stresses the importance of discreet local breeding populations connected by migration, such that recolonization is possible (effecting 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 two sub-basin groups appear to fit these criteria based on the low exchange rate of PIT-tagged individuals documented here. Behavior may keep the respective populations relatively discreet in space even though a physical conduit for continuous inter-system migration exists. One such possibility might be an innate disposition or affinity for the waters of the natal system. Once a fish enters one of the two rivers when young, there might also be a natural disposition toward upstream migration that serves to keep the fish in that river. Later establishment of a home foraging range, and fidelity to it, might strengthen this effect.

An alternative scenario might be that upstream dispersal at the confluence is random. If so, mixing of young would likely be significant and the metapopulation concept would therefore not apply and the two groups might then be considered one population. Hence, application of the metapopulation concept here must entail the assumption that larvae that drift downstream of the confluence possess a strong fidelity to the natal system and this

mechanism directs upstream traffic at the confluence, and for the most part, successfully returns fish to their respective system. To date, this has not been demonstrated or documented in any way. However, if such a mechanism was absent, and upstream migration at the confluence was random, years of high reproductive success in one river resulting in high numbers of larvae drifting downstream of the confluence, would later benefit both rivers when the growing fish returned upstream. Hence, dynamics of the receiving population would show some correlation to those of the donor population, i.e., years of high or low relative abundance of age-5 fish in the two systems would be synchronized to some extent. To date, this has not been the case: demographic dynamics of Colorado pikeminnow in the two systems appear to behave independently. For instance, Bestgen et al. (2007) reported a complete absence of recruit-sized (400-450 mm TL) Colorado pikeminnow in the Green River system in 2003 whereas our point estimate of fish this size in the Colorado River system was higher in 2003 than in any other year studied. Hence, there might be a mechanism that keeps fish on course to the natal system when they encounter mixing waters at the confluence. 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 for the most part and the two systems can therefore be viewed as functioning as an abbreviated metapopulation.

At least one other scenario is possible: the number of young fish that return upstream to the confluence is so small that even though they enter the two rivers randomly, demographics of the receiving population are not materially affected. If such a situation exists, it could be a recent phenomenon related to increased mortality of young when they enter the predator-rich waters of Lake Powell. Historically, mixing of young downstream of the confluence followed by random upstream movements may have allowed more linkage between demographics of the two populations and the metapopulation concept may not have applied. Although all such scenarios are entirely speculative, it is hoped this discussion encourages future hypothesis testing.

Stocked Fish

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. However, the four that were caught in 2008 indicate some limited long-term survival of this group. 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 personal communication). Future monitoring of fish traps at the Grand Valley Diversion Dam on the Colorado River and the Redlands Diversion Dam on the Gunnison River will reveal whether any of the surviving stocked fish attempt to return to their stocking reach.

In light of the fact that the wild population in the Colorado River is steadily increasing in abundance through natural reproduction and recruitment and because fish ladders have been completed and diversions screened, we see no reason to continue attempts to stock hatchery-reared Colorado pikeminnow in upstream reaches. Individuals have demonstrated their ability and willingness to ascend fish ladders and colonize upstream reaches if suitable habitat exists. Re-establishment objectives might be better served with habitat improvement efforts such as predator control, flow management and temperature augmentation.

SUMMARY AND CONCLUSIONS

1) The Colorado River population of Colorado pikeminnow increased in abundance since the start of the 1992–2005 mark-recapture monitoring program. Annual point estimates, with associated wide confidence intervals, tend to vary from year to year making it difficult to have confidence in any one number. However, we found a significant positive trend in the annual abundance estimates for Colorado pikeminnow $\geq$ 450 mm TL. The combined-reach point estimate for fish > 450 mm TL in 2005 was 889.
2) The Huggins estimator from Program MARK produced combined–reach abundance point estimates about 14% higher and with narrower confidence intervals than estimates produced earlier with models M_o and M_t from Program CAPTURE. The minimum AIC_c model included a reach effect on survival and fish total length as a quadratic model, but no time effect.
3) Capture probability was higher in the lower reach than in the upper reach and varied by fish size, with fish 750 mm TL being 3–4 times more susceptible to capture than the smallest fish (250 mm TL).
4) Capture probability was generally lower during the most recent 3-year study period than during the two earlier 3-year study periods, despite additional effort.
5) Survival was higher in the upper reach than in the lower reach and varied with fish size, with the highest rates for fish about 450–650 mm TL (about 80% in the lower reach; 89% in the upper reach). The lowest survival rates were for the very largest (and oldest) fish (> 850 mm TL) suggesting that mortality increased with old age. However, for fish 850 mm TL, annual survival was still 80% in the upper reach.
6) Combined-reach, annual, survival rates appeared to decline during the three study periods, from 88% (1991–1994) to 86% (1998–2000) to 80% (2003–2005) for fish $\geq$ 500 mm TL, but differences among periods were not significant. This trend, if real, has serious implications for the future viability of the population. However, conclusions should not be drawn until future assessments indicate a significant decline in adult survival has indeed occurred.

7) Self-sustainability of the population was evidenced not only by a significant positive slope in annual adult abundance estimates, but also by annual abundance estimates of sub-adults (those 400–449 mm TL) about to recruit that indicated recruitment exceeded estimated adult mortality in six of the nine years for which data were available. Although a net gain of 332 adults was estimated for the nine years studied, lapses in sampling years between multi-year efforts precluded estimating the total net gain for the period 1992–2005. Also, precision of estimates for this size group was low. Hence, although the direction of results (a net gain) is supportive of the general upward trend indicated for adult abundance, little confidence can be placed in the size of the gain estimated from this analysis.

8) Our ability to detect a significant decline in abundance from one point estimate to the next is limited by the precision of our estimates. Assuming future adult abundance estimates have mean precision similar to that of our estimates during the most recent two multi-year sampling periods (CV = 15%), declines of 30% over a specified interval would be required to be significant at $\alpha = 0.05$ and 24% at $\alpha = 0.10$.

9) ISMP electrofishing catch rates combined with those from this study, failed to track the upward trend in abundance that we detected using mark-recapture techniques. However, the comparison between the two techniques was inconclusive because electrofishing protocols in recent years deviated from those used in earlier ISMP monitoring. Nevertheless, catch rate metrics may be susceptible to biases associated with temporal variation in capture probability, a problem not shared by mark-recapture abundance estimation techniques.

10) Results of efforts to link pulses of 300-400-mm-long Colorado pikeminnow to individual year-classes suggested that high catch rates of young-of-the-year in 1996 did not later result in strong recruitment to the adult population. If true, relative abundance of fall YOY may not always be a good predictor of later recruitment. Environmental factors that influence survival of juvenile age-classes may be just as important in determining recruitment levels as factors that influence levels of larval production and survival of early life stages.

11) Body condition, an indirect indicator of forage availability and perhaps other factors, significantly declined between 1994 and 1998 but significantly increased again between

2000 and 2003. Earlier interpretations of lowered body condition signaling that carrying capacity had been reached were not supported by additional years of data. We found no correlation between levels of abundance and mean body condition.

12) Some Colorado pikeminnow moved between the Colorado River and Green River systems. Thirty-three inter-system movements between 1990 and 2005 were documented from capture-recapture records obtained from the Recovery Program's PIT tag database, representing 1.42% of the 2,117 unique Colorado pikeminnow that were captured two or more times. If it is assumed that many of these migrants spawn in a river other than their river of origin, genetic exchange may be substantial. However, 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. Hence, the interaction of the two populations fit those of a metapopulation.

13) 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 dispersed downstream into the study area and probably beyond. Forty-five fish stocked in 2004 were found in 2005. A mark-recapture estimate of the total number in the study area at that time was 192, or 3.7% of the total number stocked (5,084). Most stocked fish were found in the lower reach, some near the confluence with the Green River. No fish from the 2003 stocking were found. No stocked fish have since been found in the upstream reaches in which they were stocked, but four were found within our study area in 2008, indicating some survival and retention within the Colorado River.

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. Electrofishing catch-rate indices do not take temporal variation in capture probability into account and thereby may provide misleading results.

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 boat launches be installed at the upper and lower ends of the reach between Government Highline and Price-Stubb dams. With the Price-Stubb fish ladder now in place, the closure assumption will be violated if marked fish move into this reach and are not sampled. Currently, there is no boat access that allows sampling of this reach.
4) We recommend that if numeric recovery goals for Colorado pikeminnow in the Colorado River are to remain set by carrying capacity of the system, a better assessment is needed of what constitutes carrying capacity there. If persistent declines in mean relative body condition are to be used as an index, the capacity of the study area, not including habitat upstream of the Price-Stubb and Redlands dams, was not reached during this study when estimates of individuals $\geq$ 450 mm TL totaled 889.
5) We recommend that the consequences of using program CAPTURE models versus more complex models within program MARK be evaluated, perhaps by the population estimation ad-hoc group. Although Colorado pikeminnow monitoring in the Colorado and Green river systems now employ models within MARK, the benefits of applying these models to humpback chub monitoring should be assessed.
6) We recommend that mark-recapture abundance estimation be employed for monitoring progress of razorback sucker population reestablishment in the Colorado River. Razorback sucker capture data is already collected concurrently with Colorado pikeminnow sampling and additional field effort would not be required. Funding would be required for a biostatistician versed in abundance estimation models and a principal investigator to manage the data, work with the biostatistician, and write a final report.
7) We recommend that no additional Colorado pikeminnow be stocked in the upper Colorado or Gunnison rivers.
8) We recommend that a feasibility study be initiated to determine whether a mark-recapture population estimate can be developed for the Gunnison River. Past efforts have had difficulty catching a sufficient number of individuals over a short period to make such an

estimate practical. Now that the Redlands fish ladder has been in place for 13 years, it might be worthwhile to see how many Colorado pikeminnow have taken up residence upstream of the diversion. A pilot study, perhaps consisting of one field season, might be accomplished in a year of non-sampling in the mainstem Colorado River.

9) We recommend annual larval production be monitored in the Colorado River using drift net sampling as is currently done in the Green River system. Annual YOY monitoring in the lower reach has already been reinitiated. Understanding factors affecting larval production may aid our understanding of YOY abundance and factors that ultimately affect recruitment.

10) We recommend initiating a study that develops a more reliable means of determining the year of origin of individuals 300-400 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 lengths of Ages 2-7 are from measurements of fish aged using scales. Insufficient captures of Age 2 fish precluded estimates of growth increments between ages 1 and 2, and 2 and 3. Growth increments for fish between ages 7 and 8 were not calculated because presumptive Age 8 fish could not be reliably aged. Table and caption from Osmundson et al. (1997).

Age		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		
2	1	181.0			2-3		
3	3	232.7	190-259	37.3	3-4	82.0	56.0
4	6	314.7	267-374	41.8	4-5	61.5	53.4
5	19	376.2	326-453	33.3	5-6	47.9	45.3
6	10	424.1	375-472	30.6	6-7	32.2	36.6
7	7	456.3	430-479	20.0			

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

Year	$\hat{N}$	Lower CI	Upper CI	SE	M_{t+1}	CV
			Lower reach			
1992	480.1	151.4	1,714.2	340.4	32	70.9
1993	590.1	314.1	1,203.4	213.2	88	36.1
1994	467.6	265.1	876.0	148.5	66	31.8
1998	402.2	233.2	765.2	128.2	86	31.9
1999	416.1	249.0	731.0	118.2	60	28.4
2000	487.9	275.4	901.5	152.9	51	31.3
2003	1,192.2	683.0	2,155.3	360.8	112	30.3
2004	687.1	445.1	1,093.6	161.1	89	23.4
2005	535.8	408.4	730.2	80.6	166	15.0
			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
			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

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

Year	$\hat{N}$	Lower CI	Upper CI	SE	M_{t+1}	CV
			Lower reach			
1992	159.8	48.1	617.4	121.7	12	76.1
1993	491.7	261.0	1,008.8	179.1	75	36.4
1994	317.2	179.5	599.0	101.8	48	32.1
1998	173.6	99.8	341.6	57.8	42	33.3
1999	205.7	119.6	376.2	62.5	32	30.4
2000	400.4	225.1	745.5	126.9	44	31.7
2003	336.6	182.1	657.8	115.1	39	34.2
2004	388.2	245.3	638.0	97.1	54	25.0
2005	412.1	313.1	565.8	63.2	134	15.3
			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
			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

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

Year	$\hat{N}$	Lower CI	Upper CI	SE	M_{t+1}	CV
			Lower reach			
1992	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
			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
			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

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

Year	$\hat{N}$	Lower CI	Upper CI	SE	M_{t+1}	CV
			Lower reach			
1992	230.1	70.0	856.6	169.8	15	73.8
1993	75.5	27.1	261.6	50.8	10	67.3
1994	48.0	15.9	184.5	35.7	6	74.5
1998	101.9	52.6	228.3	41.2	21	40.4
1999	132.4	70.0	269.7	47.9	18	36.2
2000	56.6	18.2	206.6	40.7	5	71.8
2003	248.5	119.7	549.2	102.2	23	41.1
2004	232.1	132.3	426.5	71.8	27	31.0
2005	23.2	7.5	202.1	33.0	6	142.0
			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
			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

Appendix Table VI. Results of the z-test to detect change in two abundance estimates.

					One-Sided ($N_2 < N_1$)		
CV	N_1	SE(N_1)	N_2	SE(N_2)	z	P	% decline
0.25	1000	250	1000	250	0.0000	0.5000	0
0.25	1000	250	950	237.5	0.1450	0.4424	5
0.25	1000	250	900	225	0.2973	0.3831	10
0.25	1000	250	850	212.5	0.4572	0.3238	15
0.25	1000	250	800	200	0.6247	0.2661	20
0.25	1000	250	750	187.5	0.8000	0.2119	25
0.25	1000	250	700	175	0.9831	0.1628	30
0.25	1000	250	650	162.5	1.1738	0.1202	35
0.25	1000	250	623	155.75	1.2799	0.1003	37.7
0.25	1000	250	600	150	1.3720	0.0850	40
0.25	1000	250	550	137.5	1.5772	0.0574	45
0.25	1000	250	534	133.5	1.6443	0.0501	46.6
0.18	1000	180	1000	180	0.0000	0.5000	0
0.18	1000	180	950	171	0.2014	0.4202	5
0.18	1000	180	900	162	0.4129	0.3398	10
0.18	1000	180	850	153	0.6349	0.2627	15
0.18	1000	180	800	144	0.8676	0.1928	20
0.18	1000	180	750	135	1.1111	0.1333	25
0.18	1000	180	717	129.06	1.2777	0.1007	28.3
0.18	1000	180	700	126	1.3654	0.0861	30
0.18	1000	180	650	117	1.6303	0.0515	35
0.18	1000	180	648	116.64	1.6411	0.0504	35.2
0.18	1000	180	600	108	1.9055	0.0284	40
0.18	1000	180	550	99	2.1905	0.0142	45
0.15	1000	150	1000	150	0.0000	0.5000	0
0.15	1000	150	950	142.5	0.2417	0.4045	5
0.15	1000	150	900	135	0.4955	0.3101	10
0.15	1000	150	850	127.5	0.7619	0.2230	15
0.15	1000	150	800	120	1.0412	0.1489	20
0.15	1000	150	759	113.85	1.2798	0.1003	24.1
0.15	1000	150	750	112.5	1.3333	0.0912	25
0.15	1000	150	700	105	1.6385	0.0507	30
0.15	1000	150	699	104.85	1.6447	0.0500	30.1
0.15	1000	150	650	97.5	1.9564	0.0252	35
0.15	1000	150	600	90	2.2866	0.0111	40
0.15	1000	150	550	82.5	2.6286	0.0043	45
0.094	1000	94	1000	94	0.0000	0.5000	0
0.094	1000	94	950	89.3	0.3856	0.3499	5
0.094	1000	94	900	84.6	0.7907	0.2145	10
0.094	1000	94	850	79.9	1.2159	0.1120	15
0.094	1000	94	843	79.242	1.2770	0.1008	15.7
0.094	1000	94	802	75.388	1.6432	0.0502	19.8
0.094	1000	94	800	75.2	1.6614	0.0483	20
0.094	1000	94	750	70.5	2.1277	0.0167	25
0.094	1000	94	700	65.8	2.6146	0.0045	30
0.094	1000	94	650	61.1	3.1219	0.0009	35
0.094	1000	94	600	56.4	3.6489	0.0001	40
0.094	1000	94	550	51.7	4.1947	0.0000	45

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, Yampa, and Duschene), 1991–2005.

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[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	2
Green	51.5	1991 05-08	330	Colorado	183.3	2000 05-01	587	235	9

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[c]	52.5	1994 05-10	458	Gunnison	3.0	1996 08-15	579	226	2
Gunnison[c]	3.0	1996 08-15	579	Green	0.5	2001 03-21	694	173.5	5
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	80.4	2001 05-23	721	Colorado	67.0	2004 04-14	773	147.4	3
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

[1]River 1 – river fish was last captured in prior to moving to River 2
[2]River 2 – river fish moved to after last capture in River 1
[3]RMI 1 – river mile location (measured from mouth of respective river) of last capture in River 1
[4]RMI 2 -- river mile location (measured from mouth of respective river) of first capture in River 2
[5]Date 1 – date of last capture in River 1
[6]Date 2 – date of first capture in River 2
[7]TL 1 – length (mm) of fish at last capture in River 1
[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

Cover Photos:

Top: The Colorado River near rk 55 (rm 34); looking upstream towards Shafer Canyon and Dead Horse Point, Utah, 2008. Photo by D. B. Osmundson ©

Bottom: Young Colorado pikeminnow *Ptychocheilus lucius*. Photo by J. Ferreira

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