

**POPULATION STATUS OF COLORADO
PIKEMINNOW IN THE GREEN RIVER BASIN,
UTAH AND COLORADO**

Larval Fish Laboratory Contribution 140

August 2005

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GREEN RIVER BASIN, UTAH AND COLORADO**

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EXECUTIVE SUMMARY

Multiple-pass, capture-recapture sampling was conducted in most (819 river km) warm water reaches of the Green River Basin, Utah and Colorado, to estimate demographic parameters for recruit-sized (400 to 449 mm TL) and adult (≥ 450 mm TL) Colorado pikeminnow *Ptychocheilus lucius*. Three or four sampling passes were completed in each year for the Yampa, middle Green, and White River reaches (2000 to 2003), and the Desolation-Gray Canyon and lower Green River reaches (2001 to 2003). Parameter estimates derived from a Huggins robust-design multi-strata model suggested an apparent decline in abundance of Colorado pikeminnow throughout the Green River Basin, Colorado and Utah, over the study period. Based on the trend in annual point estimates from 2000 to 2003, reductions were most severe in the middle Green River (59 %) and the White River (63 %). Those reaches supported the highest number of Colorado pikeminnow in the Green River Basin. Apparent reductions in abundance were less severe in the Yampa River (29%), Desolation-Gray Canyon (11%), and lower Green River (36%) reaches, which supported smaller populations of Colorado pikeminnow. In 2001 when the entire basin was sampled, adult Colorado pikeminnow abundance was estimated at 3,304 (95% CI, 2,900 to 3,707), declined to 2,772 (95% CI, 2,216 to 3,325) in 2002, and continued to decline in 2003 to 2,142 fish (95% CI, 1,686 to 2,598), a 35% reduction. Confidence limits for basin-wide estimates in 2001 and 2003 did not overlap. Assuming year 2000 population abundance in Desolation-Gray Canyon and lower Green River reaches when no sampling occurred was similar to 2001 (estimated abundance of 1,054 adults in 2001), basin-wide adult Colorado pikeminnow abundance estimates apparently declined from 4,084 in 2000 (3,030 in middle Green, Yampa, and White rivers in 2000, 95% CI, 2,467 to 3,592) to 2,142 in 2003, an apparent reduction of 48%.

Abundance estimates for recruit-sized fish during 2000 to 2003 sampling in the Green River Basin averaged 8.9 % (4.7 to 13.3 %) of the estimated abundance of adult Colorado pikeminnow; recruitment rates may not be sufficient to offset mortality rates of adults. This suggested that apparent declines in abundance of adult Colorado pikeminnow in the Green River Basin in 2000 to 2003 were caused, in part, by lower recruitment rates. Reduced abundance of recruit-sized Colorado pikeminnow noted during this study may be due to weak year-classes of age-0 Colorado pikeminnow produced in the past several years in nursery areas of the middle and lower Green River.

Average survival rate estimated for the average-size Colorado pikeminnow from 2000 to 2003 interval was 0.65 (95% CI 0.586 to 0.708). Few captures and recaptures were made for fish ≥ 800 -mm TL, which resulted in very low apparent survival rates for those fish. The average survival rate for adult Colorado pikeminnow from 2000-2003 was lower than the 0.82 (95% CI, 0.709 to 0.89) rate estimated for Colorado pikeminnow from Interagency Standardized Monitoring Program (ISMP) data collected from 1991 to 1999. This suggested that apparent declines in abundance of adult Colorado pikeminnow in 2000 to 2003 were caused, in part, by lower survival rates in those drought years. There was no support for the hypothesis that reduced survival of adult Colorado pikeminnow was due to sampling mortality.

Apparent reductions in abundance of adult and recruit-sized Colorado pikeminnow in the Green River Basin may be due to low, drought-related base flows that began about the same time this investigation began. Flows were particularly low in the Yampa and White rivers. The precise mechanism for the apparent correlation between reduction in Colorado pikeminnow abundance and low flows is unknown. Reduced habitat area may have also increased potential

for encounters with non-native predators such as northern pike *Esox lucius*, but only in the Yampa and middle Green River reaches, because pike were rare elsewhere.

We recommend continuing with the sampling protocol for Colorado pikeminnow in the Green River Basin as called for in the Recovery Goals. Increased sampling effort may be needed during the next abundance estimation sampling period in some areas to fill in small sampling gaps and increase precision of estimates. Means to obtain higher probabilities of capture of Colorado pikeminnow in reaches where abundance estimates were relatively imprecise, such as increasing effort or adding alternative gears, should also be investigated. A better understanding of factors that influence adult survival rates and the link between abundance dynamics of early life stages of Colorado pikeminnow and recruitment to later life stages would assist managers tasked with conservation of Colorado pikeminnow.

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INTRODUCTION

Demographic parameters that describe birth, movement, and mortality rates, and population abundance are useful to understand dynamics and status of animal populations. Responses of those population parameters to biotic or abiotic drivers are of interest to ecologists attempting to understand the fundamental basis for population change. They are also useful to managers attempting to maintain or enhance abundance of free-ranging animal populations, particularly when the species of interest is rare.

Endangered Colorado pikeminnow *Ptychocheilus lucius*, is a large, migratory, and predaceous cyprinid endemic to the Colorado River Basin. Once widespread and abundant throughout warm-water reaches of the basin, wild Colorado pikeminnow are presently restricted to the Upper Colorado River Basin in the San Juan, Colorado, and Green River sub-basins. Reasons for decline of Colorado pikeminnow center mainly on negative effects of habitat alteration from river regulation and non-native fishes (Minckley 1973; Carlson and Muth 1989; Tyus 1991). Over 140 main stem and tributary dams and reservoirs and several trans-basin water diversions provide agricultural and municipal water supplies to a rapidly expanding human population and have transformed water in the Colorado River Basin into one of the most tightly controlled supplies in the world (Iorns et al. 1965; Carlson and Muth 1989). Effects of main stem dams on biota have been particularly damaging because they restrict movements of fishes such as Colorado pikeminnow, reduce seasonal variability of discharge, water temperature, and sediment load, and increase daily hydrograph variation (Vanicek and Kramer 1969; Holden 1979; Ward and Stanford 1979; Stanford et al. 1996; Poff et al. 1997). No fewer than 60 non-native fishes have been established in the Colorado River Basin, many of which prey upon or compete with various life stages of native species (Carlson and Muth 1989; Ruppert et al. 1993). The

outcome of these environmental and biotic changes for the highly endemic fish fauna of Colorado River Basin has been dramatic: two of the 35 native species in the basin are extinct, an additional 18 are federally listed as threatened or endangered or are very rare, and most others are listed by one or more basin states as declining (Stanford and Ward 1986; Carlson and Muth 1989; Bezzerides and Bestgen 2002; Mueller and Marsh 2002). Colorado pikeminnow is federally listed as endangered under the Endangered Species Act of 1973, as amended (U. S. Fish and Wildlife Service 1974).

Colorado pikeminnow, endangered bonytail *Gila elegans*, humpback chub *Gila cypha*, and razorback sucker *Xyrauchen texanus* are the focus of the Recovery Implementation Program (RIP) in the Upper Colorado River Basin (Wydoski and Hamill 1991). Recovery goals for Colorado pikeminnow provide criteria that must be achieved before downlisting or delisting can be considered (U.S. Fish and Wildlife Service 2002). The recovery criteria include demographic attributes that describe the required number of sub-basin populations and individuals (adults and juveniles) within each population, and recovery factor criteria that are directly linked to management actions and tasks needed to minimize or remove threats.

Maintenance of a metapopulation is central to Colorado pikeminnow recovery, and demographic criteria require “a genetically and demographically viable, self-sustaining population in the Green River sub-basin; and self-sustaining populations that meet or exceed estimated carrying capacity either in only the upper Colorado River sub-basin, or in both the upper Colorado River sub-basin and San Juan River sub-basin”. For consideration of downlisting or delisting, specific demographic criteria for the Green River sub-basin portion of the Colorado pikeminnow metapopulation require that, over the specified monitoring period, (1) trends in abundance estimates for adults (≥ 450 -mm total length, TL) in both the middle and

lower Green River do not decline significantly, (2) estimated mean recruitment of fish 400 to 449-mm TL (recruit-sized fish) equals or exceeds estimated mean annual adult mortality for the sub-basin, and (3) each abundance estimate for the sub-basin exceeds 2,600 adults (U.S. Fish and Wildlife Service 2002).

Our goal was to obtain accurate and precise abundance estimates for Colorado pikeminnow in the Green River sub-basin. Study objectives listed in separate research proposals for the middle and lower Green River abundance estimates to achieve that goal were summarized as follows:

1. Complete three or more sampling passes through the study area to capture recruit-sized and adult Colorado pikeminnow,
2. Obtain highest possible rates of capture of Colorado pikeminnow within concentration habitats and maximize number of individuals marked on each sampling occasion,
3. Obtain estimates of probability of capture and abundance for Colorado pikeminnow in each reach and for the entire study area,
4. Evaluate abundance of Colorado pikeminnow in canyon reaches relative to other more intensively sampled reaches, and
5. Design a procedure for monitoring population abundance, survival, and recruitment, using data collected during the study.

This paper describes the first efforts to quantify abundance, survival rates, recruitment, and population trends for Colorado pikeminnow in the Green River sub-basin, based on sampling conducted from 2000-2003.

Status and natural history of Colorado pikeminnow.--Abundance of Colorado pikeminnow varies by more than an order of magnitude in the three occupied sub-basins of the Upper Colorado River Basin. The population in the San Juan River sub-basin, which is isolated from the remainder of the upper Colorado River Basin by Lake Powell Reservoir, is relatively small and may be extirpated (Platania et al. 1991, Holden 2000). In the Colorado River sub-basin, abundance estimates for Colorado pikeminnow were conducted from 1991 to 1994 and 1998 to 2000 using multiple-pass capture-recapture sampling. Abundance estimates for the 278-river km (RK) reach from 1991 to 1994 were variable among years but averaged about 600 sub-adult and adult fish (Osmundson and Burnham 1998). Estimates conducted from 1998 to 2000 suggested population abundance increased to about 750 sub-adult and adult fish (Osmundson 2002). Although abundance estimates for Colorado pikeminnow have not been conducted in the Green River sub-basin, that population is thought the largest in existence (Tyus 1991). That assumption is based on the larger area of occupied habitat (over 900 RK) in the Green, White, and Yampa rivers and the higher Green River sub-basin catch per unit effort (catch/effort) rates for Colorado pikeminnow gathered from 1986 to 2000, compared to the Colorado River (McAda 2002).

Historically, Colorado pikeminnow achieved 1.8 m in length and 40 kg in weight (Jordan and Evermann 1896; Minkley 1973; Tyus 1991; Quartarone 1995), although the largest individual known since intensive sampling began in the late 1970's was 1,240-mm TL (this study). Large individuals may be 35 to 50 years old, and very slow-growing, based on average growth rates of 10 mm/yr or less for recaptured individuals (Osmundson et al. 1997). Sexual maturity is not reached until five to seven years old at a length of 450 to 550-mm TL (Vanicek and Kramer 1969; Osmundson et al. 1997; Osmundson and Burnham 1998).

In the Green River sub-basin, adults migrate to two main spawning areas in late spring when snow-melt runoff subsides and water temperatures warm (Tyus 1990; Irving and Modde 2000). Migrations up to 745-RK round-trip to and from spawning areas have been documented by radio-tracking adults in spring and summer, and those fish often return to established home ranges (Tyus 1990; Irving and Modde 2000). Colorado pikeminnow in the Colorado River are much less mobile during the reproductive season and made only local movements to spawning areas (McAda and Kaeding 1991). Colorado pikeminnow typically begin spawning around the summer solstice, when flows decline to near base level and water temperatures range from 16 to 22°C (Haynes et al. 1984; Nesler et al. 1988; Tyus 1991; Bestgen et al. 1998). Eggs are deposited over geomorphically complex riffle habitat and embryos hatch within four to seven days at water temperatures of 18 to 26°C (Hamman 1981; Marsh 1985; Tyus 1990; Harvey et al. 1993; Bestgen and Williams 1994). About five to nine days later, emerging larvae are transported downstream 40 to 200-RK or more to alluvial river reaches, where they rear in low-velocity shoreline areas such as backwaters throughout the summer (Nesler et al. 1988; Tyus and Haines 1991; Bestgen 1996; Bestgen et al. 1998).

Variation in abundance of adult Colorado pikeminnow in the Colorado River was thought driven by changes in abundance of young-of-year that rear mostly in the lower portion of the river (Osmundson and Burnham 1998). Recruits move upriver as subadults and eventually establish home ranges (Osmundson et al. 1998), apparently in response to a productivity gradient that increases upstream (Osmundson et al. 1998; Osmundson et al. 2002). Size-structure of Colorado pikeminnow appears stratified in the Green River sub-basin similar to that in the Colorado River (Osmundson et al. 1997), as most juveniles and sub-adults captured were found in the lower reaches of the Green River (McAda 2002). However, movement, recruitment, and

growth patterns of Colorado pikeminnow, based on analysis of capture-recapture data, has not been conducted in the Green River sub-basin.

Most Colorado pikeminnow exist in rivers regulated by main stem dams. Thus, flow and water temperature management in the Green, Colorado, and San Juan River main stems have focused on restoring regimes that more closely resemble historical conditions (Poff et al. 1997; Muth et al. 2000). Release of propagated Colorado pikeminnow in the Colorado and Green River sub-basins has been limited because natural populations were thought sufficient to effect recovery (Tyus 1991). Only in the San Juan River sub-basin has use of propagated fish been extensive. Another recent emphasis of the RIP was to reduce effects of non-native fishes, in particular, large-bodied predaceous forms. Smallmouth bass *Micropterus dolomieu* and particularly northern pike *Esox lucius*, may be a formidable threat to even large-bodied Colorado pikeminnow, particularly in the Yampa River of the upper Green River sub-basin.

STUDY AREA

The Green River sub-basin (hereafter Green River Basin unless specified) drains high-elevation areas in southwestern Wyoming, northeastern Utah, and western Colorado (Fig. 1). The study area focused mainly on warmwater stream reaches designated as critical for recovery of Colorado pikeminnow (U. S. Fish and Wildlife Service 2002), which included the lowermost 193 RK of the Yampa River, the 555.6-RK reach of the Green River (including the lower Duchesne River) downstream of the confluence of the Yampa River to the Colorado River, and the lower 167.4 RK of the White River. River geomorphology in the study area varied; relatively low gradient, depositional reaches in valleys were interspersed with higher gradient, erosive, canyon-bound reaches. Alluvial river reaches were more braided, had mostly sand or gravel

substrate, meandered to some extent within the floodplain, and were dominated by run and pool habitat. Canyon-bound river reaches were typically constrained, single-thread channels, that had a mix of riffles, runs, and pools, and a mix of substrate that ranged from sand to boulder-sized particles. River flows were highest in spring and early summer during snow-melt runoff and declined to base level by mid-summer (Fig. 2).

The Green River Basin was divided into five main reaches: the Yampa and White rivers, and three reaches of the Green River. The Yampa River reach was 118-RK long and extended from RK 192 to 74; few Colorado pikeminnow have been documented upstream of that area (Holden and Stalnaker 1975). The canyon-bound lower reach of the Yampa River (74 RK) was excluded because few fish were thought to occur there outside of the spawning season, and because logistical constraints prevented extensive sampling there (Holden and Stalnaker 1975). We were unable to conduct supplemental sampling planned in autumn for most canyon reaches during this study because of low water levels. The sampled reach of the Yampa River flowed mostly through alluvial valleys but included Little Yampa Canyon in the upper portion of the study reach. The 5 RK-long Cross Mountain Canyon and the 3 RK-long Juniper Canyon were not sampled because they were inaccessible. The Yampa River reach was sampled by personnel from the Larval Fish Laboratory, Colorado State University.

The middle Green River study reach was 143-RK long and extended from RK 539.4 (16.2 RK downstream of the confluence of the Yampa River confluence) downstream to just above Desolation Canyon at RK 396 (near the White River confluence). The reach was in an alluvial valley, with the exception of Split Mountain Canyon (RK 528.2 to 513.8), which was sampled infrequently. The 16.2 RK-long Whirlpool Canyon reach from the confluence of the Yampa River downstream to upper Island Park was also excluded from sampling. Most of the

relatively short reaches within the study area that received only cursory sampling in this study historically held few Colorado pikeminnow (Holden and Stalnaker 1975). The middle Green River reach was sampled by the Utah Division of Wildlife Resources, Vernal, Utah.

The White River study reach was 167.4-RK long and extended from just below Taylor Draw Dam downstream to the confluence with the Green River. Although Colorado pikeminnow historically occurred above Taylor Draw Dam, few or none are thought to occupy that reach since the reservoir began filling in 1984 (Martinez 1986; Martinez et al. 1994). The White River winds through alluvial valleys interspersed with short bluffs. The U. S. Fish and Wildlife Service, Vernal, Utah, was responsible for sampling the White River and the Desolation-Gray Canyon reach of the Green River (below).

The Desolation-Gray Canyon Green River reach was 189.8-RK long and extended from the head of Desolation Canyon at RK 395.9 downstream to near the lower end of Gray Canyon at RK 206.1. That reach was mostly canyon-bound and geomorphically constrained. The reach between RK 206.1 (at Tusher Diversion) and 193.2 was usually not sampled because of logistical constraints.

The lower Green River reach was 193.2-RK long and extended from near the town of Green River downstream to the confluence with the Colorado River (RK 0), and passed through the low-gradient Labyrinth and Stillwater canyons. The Utah Division of Wildlife Resources, Moab, Utah, was responsible for sampling there.

During low flow periods in all reaches, low-velocity habitat was near shore, in small eddies and pools, and behind or adjacent to mid-channel sand or gravel bars. When flows were elevated by snow-melt runoff in spring, main channel velocities were swifter, and low-velocity

areas were more limited, often consisting of flooded tributary mouths and canyons washes, and a few large backwaters.

Additional areas not sampled that may harbor Colorado pikeminnow included smaller tributaries such as the Price, San Rafael, upper Duchesne, and Little Snake rivers (McAda et al. 1980; Wick et al. 1991; Hawkins et al. 1996; Cavalli 1999; Muth et al. 2000). Adult Colorado pikeminnow in those areas were thought relatively rare compared to larger main stem reaches because habitat size was small or occupied reaches were short and use was only seasonal. The Green River in Lodore Canyon upstream of the Yampa River was also known to support adult Colorado pikeminnow (Bestgen and Crist 2000; Kitcheyan and Montagne 2005). Supplemental sampling conducted there and in other reaches in some years when abundance estimation sampling was being conducted will be discussed.

METHODS

Sampling and fish handling.--Sampling for abundance estimation was conducted in spring in each year from 2000 to 2003 in the Yampa River, White River, and middle Green River study reaches, and in each year from 2001 to 2003 for the Desolation-Gray Canyon Green River reach and the lower Green River reach. We used Pollock's robust design to allocate sampling effort (Pollock 1982; Pollock et al. 1990). This was accomplished by conducting three or four short-term sampling occasions (usually 7 to 11 days each) through each reach at approximately the same time in spring of each year, and repeating that design over the remainder of the study years. Short-term sampling occasions were conducted in spring between the time when ice off occurred and prior to or during spring runoff before Colorado pikeminnow spawning migrations began. Using hard-bottomed boat (Yampa, middle Green, and lower Green reaches) or inflatable

raft-based (White River and Desolation-Gray Canyon Green River reaches) electrofishing as the standard technique, sampling during each occasion began at the top of each reach and proceeded downstream. Electrofishing units were either pulsed-DC Coffelt or Smith-Root types, with one or two anode booms with spheres. Two boats were typically used on each sampling occasion, one on each shore, and one or usually two netters captured stunned Colorado pikeminnow. All nearshore habitat that was likely to hold Colorado pikeminnow was electrofished.

Approximately 7 to 10 d elapsed between short-term sampling occasions in each reach and year to allow for sufficient mixing of marked and unmarked fish. In the Yampa River in 2000, only a single electrofishing boat was used, but that effort was supplemented with passive sampling gears such as fyke nets and trammel nets in low velocity areas. A block-and-shock technique was sometimes used, where a large, nearshore, quiet-water area was isolated from the main channel with a trammel net and electrofishing commenced inside the block net. Colorado pikeminnow were captured by netters or in trammel nets as they attempted to leave the backwater for the main channel. Use of these techniques was limited in other years and reaches.

In most reaches, sampling focused only on Colorado pikeminnow, although other endangered fishes, and non-native northern pike, were sometimes captured. Colorado pikeminnow were measured (TL, nearest mm), weighed (nearest g), scanned for the presence of a PIT tag, and unmarked fish (>150 mm) received a PIT tag inserted into the body cavity just posterior to the pelvic girdle. The initial capture and release location (nearest 0.1 RK) was determined from river maps and a Global Positioning System unit and all Colorado pikeminnow were released within 0.15 km of their capture location.

Additional data utilized in this study was from an Interagency Standardized Monitoring Program (ISMP, McAda 2002). The ISMP sampled adult and sub-adult Colorado pikeminnow

from ten reaches (8 to 25 RK-long) of the Green River Basin, five from the Green River (RK 539.4 to 526.5, 513.6 to 483, 418.6 to 394.5, 185.2 to 154.6, 90 to 64), three from the Yampa River (RK 167.4 to 153, 128.8 to 112.7, 86.9 to 78.9), and two from the White River (RK 169.1 to 153, 33.8 to 0). The reaches totaled about 23% of critical habitat of Colorado pikeminnow in the Green River Basin and were chosen because they were accessible by a flat-bottom boat and represented reaches known to support Colorado pikeminnow. Sampling was conducted during spring each year from 1986 to 2000 when water levels were rising due to snow-melt runoff but were usually below peak runoff levels. A single electrofishing sampling pass was made down each shoreline, stunned Colorado pikeminnow were captured with dipnets, and electrofishing time was recorded. Captured fish were tagged, measured, and released with a protocol similar to that described above for abundance estimation sampling. Sampling effort was stratified among four to eight sub-reaches of each river reach and catch per unit effort statistics were calculated for each sub-reach sample. Variances and standard errors for catch/effort indices were calculated based on those samples. Prior to 1991, Colorado pikeminnow were tagged with a Carlin dangler tag, which were presumed subject to relatively high tag loss. Therefore, data from 1986 to 1990 was not included in analyses presented here. After 1990, tag loss was considered negligible because all Colorado pikeminnow were PIT-tagged. From 2001 to 2003 abundance estimation sampling data, we designated a sampling pass as one that conformed in space and time to when ISMP sampling was previously conducted. We calculated catch/effort statistics for Colorado pikeminnow to examine trends from 1991 to 2003. To compare abundance estimates of Colorado pikeminnow with catch/effort indices, we averaged capture rates for ISMP reaches that were within the main river reaches used for abundance estimation sampling. Those annual composite ISMP catch/effort indices for the Yampa River, White River, the middle Green River,

and the lower Green River were then correlated with abundance estimates for the same reaches. No ISMP sampling was conducted in the Desolation-Gray Canyon reach of the Green River, so no comparisons were available for that reach.

Robust design for capture-recapture studies.--Robust-design sampling and analysis capitalizes on the strengths of closed and open population models used to estimate demographic parameters (Pollock 1982; Pollock et al. 1990). Sampling occasions completed at closely-spaced intervals (e.g. weeks) are used to estimate population size using closed population models. That level of sampling completed in two or more consecutive years allows for estimation of recruitment and survival rates between most years. In some reaches and years, we conducted a fourth, relatively late sampling pass. We combined fourth pass data with third pass data because using a fourth pass in the analysis created asymmetry of the capture histories and difficult model fitting. Combining data was done only after analyses showed that only a couple of fish (<<1%) moved between sampling reaches between passes within a year. Thus, potential confounding due to fish movement to spawning areas was minimized.

Statistical modeling.--The combined robust-design (Kendall 1999, Kendall et al. 1995, 1997) multistrata (Brownie et al. 1993; Hestbeck et al. 1991) model in Program MARK (White and Burnham 1999) was used to estimate annual survival in year t (S_{it}), probability of transition between reach i and j (ψ_{ij}), capture-recapture probabilities within reach i for each year t and sampling occasion k (p_{ik}), and Colorado pikeminnow abundance in each reach i for each year t (N_{it}). A multi-strata (reach) model was justified because of the sampling design and because probabilities of capture varied substantially among sampling occasions (passes) and reaches within a given year, which precluded a model to estimate river-wide abundance directly. Instead, river-wide abundance estimates were obtained by summing the separate reach estimates by year.

Standard errors for river-wide estimates were obtained from the variance-covariance matrix of the likelihood from program MARK. Probability of annual transition for each reach (ψ_{ij}) was estimated; the low frequency of transitions between sampling passes conducted in a single year did not warrant occasion-specific ψ 's.

Abundance of Colorado pikeminnow in each reach was estimated with the Huggins model estimator (Huggins 1989, 1991; Alho 1990). Abundance estimates from the Huggins model were derived by the equation M_{t+1}/p^* , where M_{t+1} is the number of unique animals captured over all short-term sampling occasions and:

$$p^* = 1 - \prod_1^n (1 - p_i),$$

where p_i is the probability of initial capture within the annual sampling season. Animals in the population that were never captured have capture probability $(1 - p)^n$ but are conditioned out (removed from) of the likelihood. The new multinomial distribution still sums to one, and because only fish that were captured are included in the likelihood, individual covariates (here TL or polynomials for such) were incorporated to estimate p , ψ , and S , where appropriate. Estimates of p^* are derived with information from both the closed-captures portion of the likelihood used for abundance estimation and from the Cormack-Jolly-Seber (CJS) component of the model used to estimate annual survival rates across all reaches. With the additional information provided about p^* from the CJS portion of the likelihood, the individual p 's per pass within the annual sampling period are identifiable based on the numbers of fish initially captured during each sampling pass within a year. Thus, we could calculate abundance estimates for river reaches and years where no animals were recaptured between passes within a single year.

The covariate TL (length at first capture) was standardized with a z transformation, i.e., standardized length (SL, but not the measure of fish standard length) for fish i was

$$SL_i = (L_i - L_{\text{mean}})/SD,$$

where L_i was the TL of an individual fish, L_{mean} was the mean TL for all fish in the population, and SD the population standard deviation of TL. The z transformation was used because the numerically small covariates that result allows for better model fitting. Because adult Colorado pikeminnow grow very slowly (Osmundson et al. 1997), use of length at first capture as the covariate was deemed appropriate for fish that may be captured several times. Inclusion of the covariate TL in abundance or survival estimation modeling was important because of the potential effects of fish size on probabilities of capture. Abundance estimators such as those in program CAPTURE (White et al. 1982) do not have the capability to use individual covariates because the likelihood includes probabilities for animals that are never captured, so the covariates are unknown. Selection between models was performed with information-theoretic procedures (Akaike's Information Criterion adjusted for small sample size (AIC_c), Burnham and Anderson 1998). Analyses demonstrated that capture probabilities were equal to recapture probabilities among the short-term and annual sampling occasions (i.e., $p_k = c_k$), so heterogeneity due to capture effects was assumed minimal. We also tested for differences in rates of capture and recapture in various models to evaluate if behavior effects (e.g., fish avoidance of boats) were influencing recapture rates. We initially also fit mixture models of Pledger (2000), which were designed to incorporate heterogeneity caused by differing probabilities of capture for different segments of the population. We abandoned these models because only higher numbers

of recapture occasions (e.g., minimum of 5) are needed to detect differences in capture probabilities among groups of animals in the same population. We also explain much individual heterogeneity by including the covariate TL in other analyses.

Survival and finite population rate of change models.—Jolly-Seber type models (recaptures only and Pradel's survival and population rate of change models) in program MARK (Cormack 1964; Jolly 1965; Seber 1965; Pradel 1996; White and Burnham 1999) were used to estimate apparent survival (1991 to 1999) and population rates of change (λ , 1991 to 2003), respectively, for Colorado pikeminnow captured in the Green River Basin. Apparent survival rates (S) are the joint probability of a fish surviving from one year to the next and remaining in the population available for capture. In other words, estimates from these models do not distinguish a fish that died in the study area from one that survived and moved from the study reach to an unsampled reach. Because of that, survival rates obtained from ISMP data are likely conservative (low) because capture data were gathered from reaches that represent only about 23% of the basin. Thus, Colorado pikeminnow that move out of reaches sampled by ISMP and are never recaptured would be treated as mortalities. These models are also not able to distinguish if fish that were previously captured were able to avoid subsequent recapture by some behavioral change mechanism. Such a behavioral change would result in reduced capture probability and lower apparent survival rates. Assuming that no behavioral change occurred, survival rates obtained from 2000-2003 during abundance estimation sampling likely approached true survival, because nearly all the Green River Basin habitat where Colorado pikeminnow likely occurred was sampled. The goal of survival analyses was to determine if a composite, and perhaps conservative, survival rate from 1991 to 1999 was different than survival in the 2000 to

2003 period. Differences in survival rates over time may be useful to interpret trends in population abundance.

We used Pradel's model (Pradel 1996) to estimate λ , the finite rate of population change, which is defined as:

$$\lambda_i = N_{i+1}/N_i = \phi_i + f_i,$$

where N is population size at time i or $i + 1$, ϕ_i is survival rate, and f_i is the number of fish recruited to the population at time i per adult in the population at time i . A λ_i value less than one indicated a declining population, $\lambda_i > 1$ indicated an increasing population, and λ_i of 1 indicated a stable population. Functionally, the Pradel model is similar to the Jolly-Seber model used to predict survival rates but uses the capture history in reverse order to predict the probability of entering the population (Nichols et al. 2000). A main assumption of this model is that study area size is constant over the sampling period, which precluded the use of capture data from other ISMP reaches in some years. Global models that fit parameters (p , S , λ) for all years and river reaches were compared with models with a reduced parameter set. The AIC_c for small samples was used as a guide in model selection. We were careful to guard against overfitting models with the sometimes sparse data available for some reaches or rivers and focused on those that gave reasonable estimates of parameters that were critical to understanding the status of Colorado pikeminnow in the Green River Basin.

RESULTS

River reach abundance estimates.--A total of 3,800 Colorado pikeminnow was captured in the 42 sampling occasions (passes, includes fourth pass fish) of the five reaches during sampling from 2000-2003 (Appendix I). Of those fish captured, 3,212 (84.5%) were captured in only one year and not seen in any other year, 532 (14%) were captured in each of two years, 48 were captured in three years (1.3%), and only eight fish (0.2%) were captured in all four sampling years (Table 1). We estimated abundance of Colorado pikeminnow adults and recruits in each of the five river reaches of the Green River Basin for each sampling year to determine spatial abundance patterns and temporal dynamics. A set of eleven models was fit to the data to examine the importance of year-specific apparent survival (S), reach transition probabilities (ψ , probability of a fish moving from one reach to another), and capture probabilities (p 's, Table 2). The top model in the set of eleven contained 35% of the AIC weight, with the only competing model (# 2) differing in the degree of the polynomial of TL used to model capture probabilities. The third-best model with variable survival over all three annual intervals had a very high and unreliable survival estimate for the 2002 to 2003 interval and was not further considered. Therefore, we made inference from the minimum AIC_c model. That model had 81 parameters and included quadratic and cubic effects of TL to model a single S over the 2000 to 2003 period (three length effects, one S , four total parameters), a linear effect of TL to model ψ (a single length effect plus 20 ψ 's, one each for fish in a given reach moving to any of the other four reaches for each of five reaches; 21 total parameters), and quadratic effects of TL to model p 's (two length effects, plus those for five reaches, three sampling passes per year, three or four sampling years depending on the reach, 56 parameters). We held effects of length on estimated parameters constant, which makes the reasonable assumption, for example, that length effects on

capture rates are similar river-wide and across years. The result was size-dependent probability of capture relationships that had similar shapes but whose magnitude varied across occasions, reaches, and years.

Based on trends in point estimates over time, abundance of adult Colorado pikeminnow showed an apparent decline in every river reach of the Green River Basin over the duration of the study (Tables 3-7, Figs. 3-7). Abundance of adult Colorado pikeminnow in the Yampa River reach was the lowest observed among the five study reaches. Point estimates declined 29% from about 317 (SE = 105) fish in 2000 to about 224 (SE = 75) fish in 2003. Overlapping confidence limits among pairs of point estimates did not suggest that any were statistically significantly different. Regression analysis of \log_e abundance as a function of time (N = 4) showed a negative relationship (\log_e abundance = $243.03 - 0.1186 \cdot \text{year}$, $r^2 = 0.85$, $p = 0.079$). Except for 2001 (CV = 15%), Yampa River estimates had relatively low precision (wide confidence intervals, CV's of 31 to 34%) owing to the low number of fish captured and recaptured. This was especially true in 2002 and 2003, when no recaptures were made of fish captured and released in each respective year. Numbers of unique animals captured in 2002 and 2003 were only a third to a fourth of those captured in 2000 and 2001 despite approximately equivalent sampling effort among years. Probabilities of capture were also very low in 2002 and 2003 (Table 8). No estimate of Colorado pikeminnow recruit abundance was available in any year for the Yampa River, because only a single recruit-sized fish was captured (year 2000).

Abundance of adult Colorado pikeminnow in the White River was higher than that observed in the Yampa River from 2000 to 2003 but estimates declined more dramatically over the study period. Estimated numbers of adult fish declined steadily from 1,100 (SE = 220) in 2000, to 746 (SE = 98) in 2001, to 643 (SE = 94) in 2002, and finally to 407 (SE = 68) in 2003, a

reduction of about 63% over the duration of the sampling period. Confidence limits for abundance estimates in years 2000 and 2003 did not overlap. Regression analysis of \log_e abundance as a function of time ($N = 4$) showed a negative relationship (\log_e abundance = $633.26 - 0.3131 \cdot \text{year}$, $r^2 = 0.97$, $p = 0.016$). Consistent with abundance estimates, numbers of unique animals captured declined steadily over the study period from 265 in 2000 to 106 in 2003. White River abundance estimates had moderately good precision, with CV's ranging from 13 to 20%.

The only abundance estimate not within expectations for all river reaches and years was for the White River in 2000. In that year, one 1,240-mm TL fish was captured, and because of the extremely low predicted probability of capturing this fish (0.000062), this individual inflated the Huggins model abundance estimate by over 16,000 individuals. That individual was removed from the data and the analysis re-run to arrive at the more realistic abundance estimate reported.

Colorado pikeminnow recruits in the White River were rare during the study period and ranged from 45 (SE = 14) in 2001 to 0 in 2003, reflecting a decline in the number of recruits in the White River during this study. Confidence limits for abundance estimates of the few recruits present in the White River 2000 and 2001 did not overlap with and were higher than estimates in 2002 and 2003. Estimates of Colorado pikeminnow recruit abundance in the White River were less precise than abundance estimates for adults, with CV's that ranged from 31 to 90%.

Abundance of adult Colorado pikeminnow in the middle Green River was the highest of any of the reaches studied in the Green River Basin but exhibited a pattern of decline similar to that observed in the White River. Adult Colorado pikeminnow abundance was high in 2000 at an estimated 1,613 (SE = 149) fish, but declined steadily to 1,184 (SE = 115) in 2001, to 834 (SE

= 151) in 2002, and 663 (SE = 107) in 2003, a reduction of 59% over the study period. Non-overlapping confidence limits for abundance estimates in year 2000 compared to those in 2002 and 2003 suggested statistically significant differences and a decline in Colorado pikeminnow abundance over the study period. Regression analysis of \log_e abundance as a function of time ($N = 4$) showed a negative relationship ($\log_e \text{ abundance} = 610.90 - 0.3018 * \text{year}$, $r^2 = 0.99$, $p = 0.003$). Numbers of unique animals captured declined from 563 in 2000 to 97 in 2002, but increased slightly to 143 in 2003. Abundance estimates for the middle Green River reach had the best precision of all reaches studied, with CV's ranging from 9 to 18%. The relatively low CV's were due to the relatively large number of captured and recaptured fish.

Colorado pikeminnow recruits in the middle Green River reach were moderately abundant in 2000 and 2001 (estimates of 107 (SE = 20) and 133 (SE = 26), respectively) but apparently declined in 2002 and 2003 (estimates of 22 (SE = 15) and 43 (SE = 16), respectively); confidence limits for estimates in all years overlapped. Estimates of Colorado pikeminnow recruit abundance in the middle Green River were less precise than abundance estimates for adults, with CV's that ranged from 19 to 70%.

Abundance estimates for adult Colorado pikeminnow in the Desolation-Gray Canyon reach of the Green River and the lower Green River reach were lower than that observed in the middle Green River reach. Abundance of adult Colorado pikeminnow was 699 (SE = 109) in 2001, 757 (SE = 165) in 2002, and 621 (SE = 129) in 2003, an 11% decline over the study period. Overlapping confidence limits among pairs of point estimates did not suggest that any were statistically significantly different. Regression analysis of \log_e abundance as a function of time ($N = 3$) showed a slightly negative relationship ($\log_e \text{ abundance} = 124.97 - 0.0592 * \text{year}$, $r^2 = 0.35$, $p = 0.595$). Numbers of unique animals captured declined from 208 in 2001 to 99 and

100 in 2002 and 2003, respectively. Abundance estimates in the Desolation-Gray Canyon reach of the Green River had relatively good precision in 2001 (CV = 16%) but relatively lower precision in 2002 and 2003 (CV's of 22 and 21%, respectively).

The Desolation-Gray Canyon reach of the Green River consistently supported the highest average annual abundance of Colorado pikeminnow recruits during the study period. Recruit abundance was mixed over the study period at 163 (SE = 33) in 2001, 72 (SE = 28) in 2002, and 152 (SE = 44) in 2003; confidence limits for estimates in all years overlapped. Estimates of Colorado pikeminnow recruit abundance in the Desolation-Gray Canyon reach of the Green River were less precise than abundance estimates for adults, with CV's that ranged from 20 to 39%.

Abundance of adult Colorado pikeminnow in the lower Green River reach was the lowest of all Green River reaches and similar to that in the Yampa River. Point estimates for adult Colorado pikeminnow abundance declined from 355 (SE = 56) fish in 2001, to 261 (SE = 51) in 2002, and to 227 (SE = 49) in 2003, a 36% reduction from 2001 to 2003. Overlapping confidence limits among pairs of point estimates did not suggest that any were statistically significantly different. Regression analysis of \log_e abundance as a function of time (N = 3) showed a negative relationship (\log_e abundance = $453.24 - 0.2236 \cdot \text{year}$, $r^2 = 0.955$, $p = 0.136$). Numbers of unique animals captured declined from 143 in 2001 to 65 and 54 in 2002 and 2003, respectively. Lower Green River abundance estimates had only moderately good precision (CV's = 16 to 22%), likely due to the relatively small population present and low capture and recapture rates.

Colorado pikeminnow recruits in the lower Green River reach were moderately common during the study period and ranged from 31 (SE = 13) in 2002 to 89 (SE = 27) in 2003, perhaps

reflecting a slight increasing trend in abundance of recruits in the lower Green River reach. Estimates of Colorado pikeminnow recruit abundance in the lower Green River were less precise than abundance estimates for adults, with CV's that ranged from 23 to 41%.

Basin-wide abundance estimates.—River-wide annual abundance estimates for Colorado pikeminnow adults (≥ 450 -mm TL) and recruits (400 to 449-mm TL) reported are the sum of annual abundance estimates for reaches in the multi-strata model. Abundance of adult Colorado pikeminnow apparently declined over the period of sampling in the Green River Basin (Table 9, Fig. 8). In 2000, when sampling was restricted to the middle Green River Basin (middle Green River, Yampa River, White River), abundance of adult Colorado pikeminnow was estimated at 3,030 (SE = 287) individuals. No sampling effort was allocated to the Desolation-Gray Canyon and lower Green River reaches that year, so no abundance estimates were possible. In 2001, when sampling was basin-wide and included Desolation-Gray Canyon and lower Green River reaches, abundance of adult Colorado pikeminnow was 3,304 (SE = 206), but abundance declined in 2002 to 2,772 (SE = 283) and to 2142 (SE = 233) in 2003, suggesting a 35% decline over the period. Confidence limits did not overlap for 2001 and 2003 basin-wide estimates.

It seems reasonable to assume that abundance of Colorado pikeminnow in unsampled Desolation-Gray and lower Green River reaches in 2000 was similar to that estimated in 2001. If one sums estimates for those reaches in 2001 (1,054) with the 2000 middle Green River estimate (3,030) and uses that as a basin wide estimate (4,084) for 2000, abundance of adult Colorado pikeminnow may have declined by as much as 48% over the period 2000 to 2003. This suggested evidence of an apparently negative trend in abundance over time for Colorado pikeminnow in the Green River. The average CV for river-wide abundance estimates for 2000 to 2003 was relatively low at 9 % (range 6 to 11%).

Abundance of Colorado pikeminnow recruits (400 to 449 mm TL) per year over the period 2000-2003 varied from 130 (SE = 36) to 412 (SE = 51), and, on average, represented only 8.9% (4.7 to 13.3%) of the number of adults present in any given year. Estimates were variable over time and perhaps suggested a stable trend for Colorado pikeminnow recruits over the sampling period. Estimates of Colorado pikeminnow recruit abundance were less precise than river-wide abundance estimates for adults, with CV's that ranged from 12 to 27%.

Survival estimates.—The best AIC model suggested a constant survival rate S for Colorado pikeminnow over the study period (Fig. 9) with a TL, TL², and TL³ terms (parameters and SE's for the function of logit S are intercept = 0.6173, SE = 0.1370; TL = 0.5606, SE = 0.2373; TL² = -0.2068, SE = 0.1140; TL³ = -0.1320, SE = 0.0665), where survival was relatively low for fish about 350-mm TL, increased for fish up to about 600-mm TL, and then declined rather dramatically for larger fish. Average S adjusted to the mean TL for Colorado pikeminnow across all river reaches was 0.65 (95% CI, 0.586 to 0.708) for the 2000-2003 study period (Table 10).

We fully investigated the apparent phenomenon that larger fish had poor apparent survival in this study with many different analyses but survival estimates for large fish consistently approached zero. Analysis of the capture history records for the 18 Colorado pikeminnow 800-mm TL or larger suggested that only two were recaptured after initial capture during this study, and both recaptures occurred within the same year. Because only recaptures across years contribute to survival analyses, this was the cause for declining survival relationships for larger fish, compared to those for 1991-1999. If some of those fish are captured in years after 2003, survival rates for that size-class may increase.

Average S for Colorado pikeminnow captured during ISMP sampling from 1991 to 1999 was 0.82 (95% CI 0.709 to 0.891), higher than that observed for 2000 to 2003. The shape of the

survival relationship was also different as the best fit model included a linear term for the covariate fish TL but not a quadratic term. An exploratory analysis revealed that an added quadratic term was positive, which indicated the slope continued to rise, rather than decline, unlike survival relationship plotted for 2000-2003 data. Mean probabilities of capture for fish used in the above survival analyses were higher in the 2000 to 2003 period compared to the 1991 to 1999 period.

Probabilities of capture.--Capture probabilities for Colorado pikeminnow generated from abundance estimation data also demonstrated a strong quadratic effect of size (parameter values and their SE's for TL and TL² terms are TL = 0.2392, SE = 0.0845; TL² = -0.1904, SE = 0.0526; intercepts for the individual reaches and their SE's are in Table 8). This is because small and large fish had relatively low capture probabilities and fish from about 500 to 600-mm TL had the highest ones (e.g., Fig. 10, Yampa River used as representative example of variation). It should be noted that estimated probabilities of capture are potentially a function of fish abundance as well as other factors (e.g., behavior or habitat use) that may make fish in a certain size class more or less available for capture. Thus, the most common size class in a population does not necessarily have the highest probability of capture. An intuitive explanation to understand how capture probabilities are used to generate abundance estimates is to simply divide the number of animals in the capture sample by the probability of capture, given the unlikely but simplifying assumption that all animals at risk of capture in the population have identical probabilities of capture. For example, if 100 animals are captured in a sample and the animals have a known and constant probability of capture of 0.10, there must be 1,000 animals in the population (100/0.10 = 1,000). In this example, each fish in the capture sample contributes equally to the abundance estimate. This assumption of non-heterogeneity among individual capture probabilities is

inherent in most estimating models in program CAPTURE. Because capture probabilities of individuals often vary spatially or over time (this study), it is useful to adjust probabilities of capture by a covariate (here TL) that is known to affect rates of capture of the animals in the sample. Use of a continuous covariate such as fish length results in different probabilities of capture for fish of different lengths, and each then contributes differently to the abundance estimate. For example, for every 500-mm-TL Colorado pikeminnow captured that has a hypothetical and relatively high probability of capture of 0.20, there must be an additional four individuals of that size in the population that were not captured ($1 / 0.2 = 5$ total pikeminnow of that size in the population). Alternatively, if a relatively larger 800-mm-TL Colorado pikeminnow was captured that has a lower probability of capture of 0.05, that means there may be an additional 19 individuals in the population that were not captured ($1 / 0.05 = 20$ total pikeminnow of that size). The abundance estimate for the population results from summing the total number of fish captured and not captured. It is important to remember that probabilities of capture are themselves estimated quantities with associated variances and their accuracy is fundamental to the accuracy and precision of abundance estimates.

As was apparent from model selection, probabilities of capture were relatively low and varied widely among sampling occasions, reaches, and years (Table 8). Maximum capture probabilities (usually for a Colorado pikeminnow about 580-mm TL) were relatively low and ranged from about 0.01 to 0.20. Average probabilities of capture were slightly higher for the White River and the lower Green River reach than for the other reaches. Average annual values of probabilities of capture were lower for most river reaches in 2002 and 2003, drought years characterized by a short run-off period and a low maximum discharge level. Average

probabilities of capture tended to remain the same or increase from passes one to three in some reaches, even when fourth pass data were not combined with third pass data.

Probabilities of transition.--Transition probabilities (ψ_{ij}) characterized the annual likelihood that tagged fish would move between the five different Green River Basin river reaches. Estimates of transition probabilities adjusted probabilities of capture because the likelihood of a fish being captured in a given reach was partially a function of its continued presence there ($1 - \psi_{ij}$). Estimates of reach transition probabilities also gave insights into rates and direction of movement of Colorado pikeminnow to and from various reaches, and how those varied with fish TL.

In general, ψ 's for Colorado pikeminnow were low, especially those for non-adjacent reaches (e.g., lower Green River to the White or Yampa River, Table 11). Reaches in the middle of the study area had the most fish moving in. For example, the Desolation-Gray Canyon reach of the Green River was the only reach to have fish moving there from every other reach. The negative slope for ψ covariate TL reflected that transition probabilities among reaches were higher for smaller than larger fish (Fig. 11). Recall that transitions may reflect relatively short-distance movements just across the boundary of one reach to another (e.g., White River mouth to the middle Green River), and thus, may not necessarily reflect a large total distance moved. Average transition probabilities (only non-zero values used) for a fish of average TL moving from the Yampa River (0.027) and the middle Green River reach (0.021) were low, reflecting a relatively high propensity of fish to remain in those reaches (Table 12). The ψ from the White River (0.035), the Desolation-Gray Canyon reach (0.050), and the lower Green River reach (0.121) were higher. Mean ψ to a particular reach from all other reaches were lower for tributaries at the extremities of the Green River Basin (Yampa River = 0.012, White River =

0.027) and the lower Green River reach (0.015) than to main stem Green River sites (Desolation-Gray Canyon reach = 0.066, middle Green River = 0.054) in the middle of the study area. The negative values for net ψ from the Yampa, and lower Green River reaches, suggested a net movement of fish from those areas. The positive values for net ψ to the middle Green River and Desolation-Gray Canyon river reaches suggested a net movement of fish to those areas during this study; the near-zero net ψ value for the White River suggested equal numbers of fish entering or leaving that area.

The relatively high and positive ψ 's for relatively small fish in the lowermost two sections of the Green River (see length frequency histograms below) reflected an upstream transition rate. Estimates of ψ for fish from the lower Green River to the Desolation-Gray Canyon reach (0.121), for fish from Desolation-Gray Canyon to the middle Green River reach (0.078), and for fish from the White River to the Desolation-Gray Canyon reach (0.080) were the largest detected in this study. Upstream ψ to the White and Yampa rivers from those areas was lower. The highest downstream ψ 's detected were for fish from the middle Green River to Desolation-Gray Canyon (0.045) and for fish from the White River to the Desolation-Gray Canyon reach (0.080).

Finite population rates of change.—We attempted to fit models that estimated λ as a function of time for ISMP reaches, for middle and lower Green River reaches, and the Yampa and White rivers. Parameter estimates were imprecise or models did not converge when λ was estimated as a function of p , S , river, and time. Therefore, we dropped the river term and simply estimated a river-wide λ over time with constant p and S , which allowed valid estimates for the first and last intervals as well. We did not use the TL covariate because fish were likely to grow

substantially over capture-recapture intervals during the 1991-2003 period, which may have biased size effects over time.

Finite population rates of change (λ_i) estimated for the period 1991 to 2003 suggested a long-term expansion in abundance of Colorado pikeminnow in the Green River Basin up to year 2000 because λ_i was > 1 every annual interval except for 1996-1997 (0.80) and 1998-1999 (0.99) (Fig. 12). Confidence limits about the estimates were typically wide. For all three annual intervals between years of abundance estimation sampling from 2000-2003, λ was < 1 and the upper bounds of confidence limits did not include one in any of the three periods.

ISMP catch/effort trends, 1991 to 2003.--Catch/effort indices at standard ISMP sites for Colorado pikeminnow in the four reaches of the Green River Basin were variable but generally increased up to year 2000 (Fig. 13). White River catch/effort indices were particularly variable, as they varied by almost an order of magnitude over the duration of ISMP sampling. Catch/effort indices were highest for the White River and middle Green River reaches and lower for the Yampa River and the lower Green River reach. If catch/effort indices reflected population size, Colorado pikeminnow abundance in the Green River Basin appeared to increase rather dramatically from 1991 to 2000, particularly in the middle Green River and the White River. Catch/effort data suggested that abundance of Colorado pikeminnow in the Yampa and lower Green River reaches increased at a slower rate up to 2000. Similar to abundance estimates and λ , catch/effort indices for Colorado pikeminnow after 2000 declined in all river reaches.

Correlation of annual abundance estimates and ISMP catch/effort indices for all river reaches combined ($n = 15$, none for Deso-Gray reach) from 2000 to 2003 suggested a positive and moderately strong relationship ($r = 0.70$, $p = 0.005$). Correlation coefficients for annual abundance estimates and ISMP indices for individual river reaches were relatively strong for the

middle Green (0.95, $n = 4$) and lower Green (0.99, $n = 3$) rivers, and moderately strong for the White River (0.85, $n = 4$) and Yampa River (0.67, $n = 4$).

Length-weight and length-frequency analyses.--Mean TL of adult Colorado pikeminnow remained essentially the same in each period, 548 mm in the 1991 to 1999 period (SD = 71.2) and 544 mm (SD = 67.9) in the 2000 to 2003 period. As expected, mean TL of Colorado pikeminnow recruits was similar in each period, 428 mm in the 1991 to 1999 period (SD = 14.5) and 430 mm (SD = 15.9) in the 2000 to 2003 period. Analysis-of-covariance (ANCOVA) showed that length-weight relationships for the two groups of fish were statistically significantly different ($df = 2$, 1786, $F = 23,437.8$, $p < 0.0001$, $R^2 = 0.962$). The \log_e length - \log_e weight relationships estimated for Colorado pikeminnow 127 to 859 mm TL follow.

$$1991 \text{ to } 1999, \log_e \text{ WT} = -12.34384659 + 3.10104192 * \log_e \text{ TL}$$

(SE intercept = 0.08939953, SE slope = 0.01460265) and,

$$2000 \text{ to } 2003 \text{ group } \log_e \text{ WT} = -12.34384659 + 3.09116143 * \log_e \text{ TL}$$

(SE intercept = 0.08939953, SE slope = 0.01433866).

Differences in predicted weight for a hypothetical 600-mm TL Colorado pikeminnow showed that a fish from 2000 to 2003 was 1686 g, or about 6.5% less than a fish of the same length from 1991 to 1999 (1796 g).

Total length of Colorado pikeminnow captured from 2000 to 2003 ranged from 30 to 1,240 mm. Average TL of all captured and recaptured Colorado pikeminnow included in capture-recapture analyses was 499.4 mm (SD = 103.3, $n = 3,866$). The largest Colorado pikeminnow captured was from the White River, and it, along with two other individuals 900-mm and 980-mm TL, were the only fish captured ≥ 900 -mm TL.

Length-frequency distributions for the upstream Yampa River, White River, and middle Green River reaches (Figs. 14-16) suggested presence of a larger proportion of relatively large Colorado pikeminnow, and relatively fewer fish less than 450-mm TL. In those reaches, only 7.0% of all Colorado pikeminnow captured were less than 450-mm TL. In the Yampa River, only one Colorado pikeminnow smaller than 450-mm TL was captured from 2000-2003 (2000). In contrast, the proportion of relatively small Colorado pikeminnow increased progressively downstream in the Green River (Figs. 17 and 18). For example, from 2001 to 2003, 24.7% of the Colorado pikeminnow sampled in the Deso-Gray Canyon reach of the Green River were < 450-mm TL. In the lower Green River reach, abundance of relatively small fish < 450-mm TL (including many < 100-mm TL) was even higher, at 68% of all Colorado pikeminnow captured.

Population-structure of recruit and adult Colorado pikeminnow in ISMP samples changed between the two periods, 1991 to 1999 and 2000 to 2003 (Fig. 19). Number of Colorado pikeminnow recruits ($n = 186$) in the period 1991 to 1999 averaged 24.7% (7.9 to 58.5%) of the number of adults in samples ($n = 826$). During the period 1991 to 1999, there were four years (three from 1992 to 1994) when proportion of recruits was high (>20%), three years when proportion of recruits was moderate (>10 to 20%), and two years when it was low (0 to 10%). In the period 2000 to 2003, number of Colorado pikeminnow recruits ($n = 14$) was only 3.4% (0 to 6.6%) of the number of adults present ($n = 418$). From 2000 to 2003, proportion of recruit-sized Colorado pikeminnow was low in all four years and zero in three of those (2001 to 2003).

DISCUSSION

Comparison of the point estimates derived from capture-recapture sampling and data analysis suggested that abundance of adult Colorado pikeminnow in the Green River Basin

declined from over 3,300 fish in 2001 to about 2,142 individuals in 2003, an apparent reduction of 35%. Non-overlapping confidence limits for the years 2001 and 2003 for basin-wide Green River abundance estimates also suggested a significant decline in abundance. An even greater reduction of 48% was observed if one adds lower Green and Desolation Gray Canyon estimates from 2001 (as a measure of their year 2000 abundance), to the middle Green River estimate from 2000. Among individual reach estimates, confidence limits among Green River Basin abundance estimates from 2001 to 2003 generally overlapped with three exceptions. Those were for the largest populations, the middle Green River, when confidence limits for the relatively low 2002 and 2003 estimates did not overlap with confidence limits for the higher 2000 abundance estimate, and for the White River when the 2000 estimate was higher and the confidence limits did not overlap with the 2003 estimate. Regression of \log_e abundance estimates of Colorado pikeminnow adults as a function of time suggested strong negative relationships over time for the middle Green River and White River, and marginally significant and negative relationships over time for the Yampa River and the lower Green River. The adult Colorado pikeminnow population in the Desolation-Gray Canyon reach of the Green River showed only a slight and non-significant reduction in abundance over time. Below we discuss the abundance estimation model, model assumptions, implications of parameter estimates, and potential reasons for the apparent decline of Colorado pikeminnow abundance in the Green River Basin during the study period.

Model selection and assumptions.--We explored a series of increasingly complex models that led us to select the Huggins robust-design multi-strata model as the most realistic one for estimation. The sampling design (three or four primary annual sampling periods with three closely-spaced secondary sampling occasions in each year) led logically to a robust-design

estimator which allowed estimation of Colorado pikeminnow abundance for every sampling year and potentially, estimation of survival between years of sampling. The Huggins model allowed use of the covariate TL, which was important because fish size affected capture probabilities and survival rates of Colorado pikeminnow. Incorporation of size effects into survival and capture probabilities allowed for more efficient and realistic population modeling. Effects of TL on survival rates also revealed empirical information about the demographics of Colorado pikeminnow in the Green River Basin.

The multi-strata aspect of the estimating model was important because of the sampling design, and because differences in size-structure of Colorado pikeminnow among reaches (strata) affected capture probabilities and ultimately abundance estimates. Differences in capture probabilities across strata might also be expected because of differences in geomorphic conditions (canyon vs. valley), sampling crews, and the type of sampling craft (raft vs. boat) used in each reach. This was important because sampling crews noted differences in capture efficiency among sampling trips within a year and across years because of differences in turbidity, flow level, or availability of off-channel habitat. Finally, this model offered the further flexibility of estimating effects of fish moving from one reach to another (ψ) among years. Thus, the manner in which the data were collected and the biology of the subject animal logically led to use of this estimating model.

Fulfilling the assumptions of the underlying model is a critical first step in obtaining reliable abundance estimates. Aspects of the experimental design employed in this study ensured that most assumptions of closed-model abundance estimators were met. The assumption of demographic closure was met, in part, because within-year sampling was limited to a relatively short time period in spring prior to Colorado pikeminnow migration to spawning areas. This

reduced the possibility of movement to the small areas that were not efficiently sampled. Static population size was also ensured in the period encompassed by the within-year sampling occasions, because of the large size of the study area. The only location of emigration/immigration for fish was from the distant downstream Colorado River. The likelihood of substantial movement from there is much reduced at that time of year because fish tend to occupy small and stable home ranges (Tyus 1990; Irving and Modde 2000). This notion was further supported by the low number of Colorado pikeminnow moving (ψ 's) between river reaches within a sampling season (unpublished data). The short period encompassed by the sampling occasions also ensured that mortality and recruitment were minimized.

The assumption of homogeneity of capture probabilities of individuals is unlikely to be fulfilled completely except in all but the most restricted conditions. However, we minimized heterogeneity due to fish size effects by adding the covariate TL to analyses where appropriate, which adjusted capture probabilities over the range of fish lengths encountered. This was important because sampling crews noted that large fish were sometimes more difficult to capture than small ones. We investigated the likelihood of a population composed of groups of individuals with inherently different capture probabilities but found no support for such based on preliminary analyses using mixture models (Pledger 2000). We also demonstrated that initial capture probabilities were equal to recapture probabilities among the short-term sampling occasions (i.e., $p_k = c_k$) by including an additive parameter to the top model (additive model is #4 in the set). The additive model suggested that recapture probabilities were slightly (usually about 0.001) but not importantly higher than initial capture probabilities. Minimal differences in initial capture rates and recapture rates suggested that confounding due to factors such as fish avoidance of sampling boats did not introduce heterogeneity into capture probabilities, so p 's and c 's were

held equal in Huggins models. Thus, to the extent possible, we tested for and found no effects of heterogeneity other than the effect of fish body size.

Another relevant assumption in this study is that animals mix freely between concentration habitat (backwaters, shorelines, eddies, main channel) and adjoining areas between sampling occasions such that all animals in the population are available for capture. A corollary assumption is that sampling effort was distributed over most occupied habitat. There is evidence that mixing of Colorado pikeminnow does occur between concentration areas and other habitat types among sampling occasions in the Colorado River (Osmundson and Burnham 1998). They found high probabilities of capture within concentration backwater habitat in a single sampling occasion, but relatively low probabilities of recapture in those same locations between occasions. The logical explanation for this capture pattern is that many fish moved into and out of concentration habitat between sampling occasions. In the Green River Basin during this study, we demonstrated similar mixing because initial capture probabilities were equal to recapture probabilities among the short-term sampling occasions (i.e., $p_k = c_k$). If fish were not mixing, we would expect that recapture probabilities would be much higher than initial capture probabilities, because the same shoreline habitat was sampled during each pass. We probably had poor sampling efficiency in very deep pools (> 2-m deep), but the amount of that habitat type relative to shallower, easier-to-sample areas where Colorado pikeminnow typically reside was small (Tyus and McAda 1984). Thus, short-term fish movement patterns, analysis of capture and recapture rates, and our relatively complete sampling coverage of occupied habitat likely minimized bias due to incomplete mixing of marked and unmarked animals.

We also assumed that recognition of marked Colorado pikeminnow was high (all were scanned) and that tag loss was low. Although differences in capture rates may exist because of

differences in crew experience or effort, effects of such on abundance estimates should be minimized because capture probabilities were estimated for all sampling occasions, reaches, and years.

Abundance estimates.--Consistent declines in abundance estimates over time and in every major river reach suggested a river-wide reduction in abundance of Colorado pikeminnow in the Green River Basin from 2000 to 2003. Given the absence of obvious violations of assumptions for abundance estimation models, and that river-wide estimates were relatively precise, abundance estimates presented here are considered reliable. Abundance of Colorado pikeminnow recruits was much lower than for adults and suggested that recruit abundance was not sufficient to maintain adult abundance at a stable level over the period of study. This is true because the proportion of recruits to adults in the population was much less than the proportion of adults that apparently died each year. The λ analysis also supported the hypothesis that reduced recruitment was a main reason for the apparent decline of adult Colorado pikeminnow in the Green River Basin. Recruitment dynamics for Colorado pikeminnow are episodic, occurring at intervals of several years in the Colorado River (Osmundson and Burnham 1998), and such may also be the case in the Green River.

Estimates for the Yampa River suggested a stable number of adult Colorado pikeminnow in 2000 and 2001 but abundance declined slightly in 2002 and more in 2003. Based on declines in capture rate from 2000 and 2001 (82 and 120 individuals captured, respectively, see also Fig. 13) to 33 and 31 in each of 2002 and 2003, respectively, and the presence of large, predaceous northern pike in the Yampa River, expectations may have been for lower abundance estimates. However, in each of those latter two years, not a single fish was recaptured from samples taken that year (no within year recaptures). The low probabilities of capture resulted in abundance

estimates for 2002 and 2003 that were only slightly lower than those for 2000 and 2001, in spite of small capture samples. However, with the exception of 2001, the limited number of fish captured and recaptured in the Yampa River resulted in abundance estimates that were relatively imprecise (high CV's, wide CI's) so definitive statements about the status of Colorado pikeminnow in the Yampa River were difficult to make.

Declines of adult Colorado pikeminnow in the White River and middle Green River reach appear more pronounced and were particularly important because those areas represented the largest segments of the Green River Basin population. Abundance reductions in the middle Green River reach may even be conservative given that the ψ -analysis suggested that area was a sink for Colorado pikeminnow moving from other reaches. The slope estimate for regression relationships of \log_e abundance as a function of time is an estimate of the percent annual change in the population. The negative and relatively large slope estimates for the White River and the middle Green River reach suggested that the factor(s) influencing apparent basinwide abundance declines were more acute there.

Decline in abundance of adult Colorado pikeminnow in the lower Green River reach was not as severe as in the middle Green River reach or the White River. A relatively small apparent decline in the Desolation-Gray Canyon reach occurred over the term of the study. The smaller reduction relative to the other reaches may be due to the relatively large number of Colorado pikeminnow moving into that reach annually, as shown by the transition rate estimates.

Trends in point estimates also suggested a decline in abundance of recruits for most reaches where they occurred, with the exception of the lower Green River, where they apparently increased slightly in 2003. Abundance estimates for recruits in each river reach generally had relatively broad and overlapping confidence limits.

Other evidence and analyses also supported the notion of an apparently declining population of Colorado pikeminnow in the Green River Basin during the study period. Estimates of λ greater than 1 for most years from 1991 to 2000 suggested an increasing population of Colorado pikeminnow in the Green River Basin. After 2000, λ was consistently much less than 1, which suggested a declining population. The negative rate of population change could be the result of reduced survival or recruitment of Colorado pikeminnow, or some combination of all those factors.

Trends in the ISMP catch/effort data were consistent with λ and abundance estimates and suggested a post year-2000 decline in abundance of Colorado pikeminnow in every portion of the Green River Basin. If catch/effort indices reflected abundance, the Green River Colorado pikeminnow population may be reduced to levels at or near those present in 1991. Catch/effort data for Colorado pikeminnow for individual rivers showed a positive and reasonably strong relationship with abundance estimates for middle and lower Green river reaches, and moderately strong relationships in the White and Yampa rivers. Osmundson (2002) found poor agreement with abundance estimates and catch/effort indices in the Colorado River, perhaps because of relatively poor precision of abundance estimates. Investigation of the strength of these relationships, and factors that affect those relationships, should continue in the future when more abundance estimates are gathered, because ISMP-like sampling may yet be a useful, less-intensive monitoring tool in the future.

Consistency of trends indicated by the less sampling intensive catch/effort and λ parameters compared to higher effort abundance estimation sampling suggested less costly options to monitor some demographic parameters for Colorado pikeminnow in the Green River Basin. Recall that data to estimate the λ parameters for the years 1991 to 1999 were derived

from ISMP data, which was collected from about 23% of the range of Colorado pikeminnow in the Green River basin and in one sampling pass. More precise λ estimates, inclusion of reach specific survival rates or probabilities of capture, or estimates for individual river reaches would require more intensive data collection. Decisions about appropriate monitoring tools should evaluate the costs associated with a particular technique relative to the importance and precision of the particular estimates obtained. Effects of increased sampling effort expended in capture-recapture studies relative to that for less intensive monitoring should also be considered. Even though we found no detectable effects of sampling on Colorado pikeminnow, the possibility remains that increased sampling may have undetected effects, behavioral or otherwise, on Colorado pikeminnow. Future sampling will also be instructive to determine if any of the Colorado pikeminnow > 800 mm-TL that were captured only once during this study persist.

The relatively close regression relationships between adult Colorado pikeminnow abundance and years for the period 2000-2003, for both river-wide and reach estimates, was striking because they suggested a relatively consistent rate of year-to-year decline, but one that varied among reaches. This was not an artifact of the abundance estimation model because probabilities of capture were computed for each sampling occasion, river reach, and year and S was held constant. Instead, the consistent rates of decline suggested that chronic, ongoing effects caused decline of adult Colorado pikeminnow throughout the Green River Basin. However, as noted above, rates of decline varied in various river reaches.

Survival rates.--Decline in abundance of adult Colorado pikeminnow over the study period in the Green River Basin may be attributable to reduced survival, reduced recruitment, or both. Apparent survival for the period 1991-1999 was higher than survival estimated for the more recent 2000-2003 period. The recent rate is also lower than survival rates of adult Colorado

pikeminnow in the Colorado River from 1991-1994. There, survival rates for adult fish ranged from 0.82 to 0.87 using two different analytical techniques (Osmundson et al. 1997; Osmundson and Burnham 1998). The consistently lower recent survival estimate may be at least partially responsible for declines in abundance of adult Colorado pikeminnow in the Green River Basin.

Comparison of the shape of the length-dependent survival rate curve from 1991-1999 compared to that for the 2000 to 2003 period suggested different relationships in the two periods. The 1991 to 1999 relationship showed that survival increased as a function of fish TL, eventually approaching an asymptote of 1. The asymptote near 1 was an artifact of the logit relationship as we do not reasonably expect 100% survival of larger fish. A key point was that a quadratic term added to the relationship had a positive (albeit non-significant) slope, which indicated that survival of larger and older age-classes continued to increase.

The survival relationship for Colorado pikeminnow for the 2000 to 2003 period was different than for the 1991 to 1999 period. Addition of polynomial terms showed very high survival of very small fish (we truncated the relationship at the lowest point for smaller fish at 350-mm TL), which was again an artifact of trajectory of the predictive model. We did this because it seemed reasonable that survival of smaller-bodied Colorado pikeminnow would continue to decline, similar to that for the 1991-1999 period. More importantly, the relationships that described survival of larger-bodied fish for the 2000-2003 period peaked at about 580-mm TL, after which survival rate declined. This was the result of the large effect for the negative quadratic term for the survival rate relationships. The relationship was nearly identical when the data were re-analyzed without the four largest fish (≥ 900 -mm TL) included, which suggested that the few large individuals were not the cause of the negative quadratic term. Further investigation of the capture histories showed that of the 18 fish ≥ 800 -mm TL that were captured,

none were recaptured among years (two individuals within the same year). Non-existent captures among years would cause the survival rate function to decline to near zero for the large fish rather than increase as it did for the 1991 to 1999 data. Non-existent recaptures of large individuals suggested that they were either very difficult to capture because they learned to avoid the capture gear, used habitat where capture gear was not effective, or that some individuals died.

Lower survival rates of Colorado pikeminnow in the Green River Basin in the period 2000 to 2003, particularly for larger-bodied fish, may be due to several factors including negative effects of handling (including tagging) or electrofishing, stress-induced mortality due to low streamflow levels in drought years 2002 and 2003, expanding populations of introduced predaceous fishes such as northern pike, or a combination of these and other yet undiscovered factors. Although population declines appeared consistent with increased mortality due to effects of electrofishing or handling, we did not find support for that hypothesis. The number of Colorado pikeminnow mortalities that we observed as a direct result of capture during this study were small ($N = 6$ over the entire study), so high levels of electrofishing-induced or handling-induced mortality were not evident. Colorado pikeminnow recaptured in multiple passes within a year generally appeared in good condition, with no external signs of damage (e.g., bruising), handling-induced disease (e.g., fungus), or other ill effects. We have no data to address effects of delayed mortality on Colorado pikeminnow, except that electrofishing-captured fish implanted with radio transmitters for use in telemetry studies generally have high survival (Tyus 1990; Kitcheyan and Montagne 2005).

In support of observations of healthy fish captured and recaptured in the field, independent evaluations did not suggest electrofishing was harmful to Colorado pikeminnow. Controlled laboratory studies (Meisner 1999) found minimal soft-tissue and vertebral damage from the

electrofishing fields normally used for sampling, on sub-adult Colorado pikeminnow (mean = 337-mm TL). An X-ray analysis of Colorado pikeminnow captured by electrofishing also suggested low incidence of damage to vertebrae (Hawkins 2002). Further, recapture rates of Colorado pikeminnow tagged and released throughout the Upper Colorado River Basin were not different for groups of fish first captured by electrofishing or nets (trammel or fyke nets, Hawkins 2003). A final and compelling reason that electrofishing may not be a main reason for increased mortality of Colorado pikeminnow from 2000-2003 was that the relatively high survival rate (0.82) estimated for Colorado pikeminnow in the Green River Basin in the period 1991 to 1999 was from fish that were captured and recaptured exclusively with electrofishing gear similar to that used during this study. Collectively, information presented above does not suggest that increased mortality due to electrofishing effects was the likely main cause of increased mortality of Colorado pikeminnow in the Green River Basin in the period 2000-2003. Additional years of sampling may yield information on whether large fish were in fact present in the area during sampling and were simply difficult to capture, or if they were not present.

The relatively low mortality rates estimated for Colorado pikeminnow in the Colorado River from 1991-1994 (Osmundson et al. 1997; Osmundson and Burnham 1998) were derived from fish captured exclusively by trammel nets set in backwaters. Estimates of survival during more recent capture-recapture sampling that used both electrofishing and trammel nets as capture techniques are not yet available. Comparison of survival rates of Colorado pikeminnow in the two periods when different mixes of gear types were used may shed additional light on whether electrofishing may increase mortality rates. Estimation of survival rates of Colorado pikeminnow first captured with either electrofishing or trammel nets may also be a useful technique to assess potential effects of electrofishing (Hawkins 2003).

Reduced stream flows may also be a reason for reduced survival rates of Colorado pikeminnow in the Green River Basin in 2000 to 2003. Base flows were relatively low in all years from 2000 to 2003, and particularly so in 2002 (Fig. 2). For example, mean monthly flow levels of the Green River at Jensen (gage # 09261000) in July in 2000, 2001, 2002, and 2003, were the 8th, 3rd, 2nd, and 7th lowest, respectively, that have been recorded since gage operation began in 1947; other years of low July flows were 1961 (5th), 1963 (1st), 1989 (4th), and 1994 (6th). Mean annual flows for 2000, 2001, 2002, and 2003 (water years) were the 19th, 7th, 2nd, and 9th lowest, respectively, that have been recorded in the 57 years of gage operation. Rates of decline in abundance of adult and recruit-sized Colorado pikeminnow varied in the five different reaches sampled in the Green River Basin from 2000-2003 and were highest in the middle Green River reach and the White River. The exact mechanism for increased mortality due to drought is not apparent either, but could be due to decreased habitat size, density-dependent effects of crowding of large, piscivorous Colorado pikeminnow into reduced habitat and subsequent reduced food supply, increased incidence of disease, or other unknown factors. This may be particularly true in the White River, which is the smallest stream sampled during this study.

Reduced condition of Colorado pikeminnow in 2000 to 2003 compared to 1991 to 1999, based on ANCOVA of length-weight relationships, may be responsible in part, for reduced survival in drought-affected streams. Reductions in habitat size may have also reduced survival by increased potential for encounters (direct predation or bite damage) with predaceous northern pike, which are abundant in the Yampa River and present in the middle Green River reach. Given rather severe reductions in stream flow, perhaps apparent reduced abundance of Colorado pikeminnow in the Green River Basin during the study period is not surprising.

The “apparent” portion of apparent survival estimates also merits discussion. Such estimates of survival may reflect the fact that estimates of S are the joint probability of an individual surviving, and remaining, in the reach so that it is available for sampling. Thus, if a fish moved from a sampled reach to an unsampled one and remained there, by definition, that fish represents a mortality. We did not sample about 12% of critical habitat occupied by Colorado pikeminnow in the Green River Basin. Those areas and others such as Lodore Canyon of the Green River just upstream of the Yampa River have the potential to harbor additional Colorado pikeminnow (Bestgen and Crist 2000; Kitcheyan and Montagne 2005). Although large numbers of Colorado pikeminnow have been captured in such reaches, particularly Lodore Canyon, use of those canyon areas occurred mostly in seasons other than when spring-time abundance estimation sampling was conducted. Based on telemetry and tag recapture data, most Colorado pikeminnow that moved to that area in portions of 2001, and all of 2002 and 2003, did so in summer. Most fish were from reaches such as Island Park, other downstream portions of the middle Green River reach, or even the Yampa River (Kitcheyan and Montagne 2005; K. Bestgen, unpublished collection data RIP study 115), locations which were well-sampled during abundance estimates. A few fish in 2001 moved into Lodore Canyon before summer in April and May. The few Colorado pikeminnow captured in locations such as Whirlpool Canyon also appear to have originated in areas included in abundance estimation sampling (K. Bestgen, unpublished data). Supplemental electrofishing conducted during this study in Split Mountain Canyon produced only a single Colorado pikeminnow, indicating that few fish resided there.

These movement and tag-recapture data for Colorado pikeminnow in canyons have two main implications. First, apparent survival estimates may be relatively close to true survival because fidelity to the original capture reaches was high. This is true because even though some

Colorado pikeminnow move seasonally (mostly in summer), fidelity of fish appears high to reaches sampled for abundance estimation because fish move back to those reaches by spring. Thus, the apparently low level of permanent emigration to unsampled reaches does not dramatically affect survival rates, which makes apparent S more closely approximate true S . A second implication of these data is for abundance estimates themselves. The mostly seasonal use of canyon reaches such as Lodore and Whirlpool Canyon, and likely lower Yampa Canyon, suggested that most Colorado pikeminnow moved to alluvial reaches by spring when abundance estimation sampling was conducted. This means that abundance estimates for Colorado pikeminnow for the reaches sampled in this study are likely representative for the entire Green River Basin because they are not biased by presence of large numbers of Colorado pikeminnow in unsampled canyon reaches.

Recruitment rates.--Reduced recruitment may also be responsible, in part, for the decline of adult Colorado pikeminnow in the Green River Basin. The RIP set the definition of a recruit as a Colorado pikeminnow 400 to 449-mm TL (U. S. Fish and Wildlife Service 2002). Based on expected growth of about 43 mm/yr for Colorado pikeminnow in the 400 to 449-mm TL size-class (Osmundson et al. 1997), the average recruit-sized Colorado pikeminnow would become part of the adult population the following year. The expectation of recovery goals is that recruitment will, over time, balance mortality of adults to produce a stable adult population. In other words, the adult population is maintained when the number of adults that die in year i is balanced by the number of recruits present in year $i - 1$ that survive to the following year. The percentage of recruits in samples used for abundance estimation that were collected during the period 2000-2003 (4.9 to 13.3%) suggested that recruitment was not sufficient to offset the 35%

apparent annual mortality rate ($1 - S = \text{mortality} * 100$) estimated for adult Colorado pikeminnow in the Green River Basin.

Comparison of recruit abundance in ISMP samples in two periods, 1991 to 1999 and 2000 to 2003, provided even more compelling evidence that poor recruitment played a major role in the decline of abundance of adult Colorado pikeminnow in the Green River Basin during this study. During the 1991 to 1999 period, Colorado pikeminnow recruit abundance was 24.7% of adult abundance. Given that apparent average annual mortality rate of the average-sized fish in the Green River Basin from 1991 to 1999 was about 20% ($1 - 0.80 = 0.20 * 100$), that level of recruit abundance should equal or exceed losses to mortality. Recruitment rates higher than mortality would explain an apparently expanding population of Colorado pikeminnow in the Green River Basin in the period 1991 to 1999, based on ISMP catch/effort data. Similarly, lower abundance of recruits (3.4% of adult abundance) in 2000 to 2003 (including three years at zero), coupled with higher apparent mortality rates, appears to explain, in part, the apparently declining population of Colorado pikeminnow in the Green River Basin in the period 2000 to 2003.

An implicit assumption of this recruitment scenario is that ISMP samples accurately portrayed the population structure of Colorado pikeminnow in the Green River Basin. Similarity of the percent of recruits from ISMP samples (3.4%) for 2000 to 2003 (a subset of abundance estimate data) and the proportion of recruits to adults in abundance estimates for the same period (8.9%) mostly validates that assumption. The slightly lower proportion of recruits in ISMP samples compared to abundance estimates is likely explained by the under-weighting of ISMP samples in areas that contained relatively large numbers of recruit-sized Colorado pikeminnow. Only two of 10 ISMP sampling localities (both in the lower Green River reach) were located in areas where 400-449-mm TL Colorado pikeminnow were abundant (McAda 2002; this study).

Five of 10 ISMP sampling localities were taken in the Yampa and White rivers, localities where recruit-sized Colorado pikeminnow were either absent or rare, and the remaining three ISMP localities were in the middle Green River reach. Given the relative paucity of ISMP sampling sites where recruit-sized Colorado pikeminnow were abundant, the slight discrepancy between the percent of recruit abundance for ISMP and abundance estimation data for the period 2000-2003 is easily understood.

Some have argued that because Colorado pikeminnow are long-lived and recruitment may be episodic, comparisons of recruitment in the periods 1991 to 1999 and 2000 to 2003 are not valid. A reason offered is that we simply may not have observed a recruitment event during that shorter 2000 to 2003 time period, and if one had occurred, it would balance out mortality and result in a stable population. Recruitment does, however, appear to occur with reasonable frequency, (e.g., Fig. 19), with moderate ($N = 3$) or high ($N = 4$) recruitment events occurring in seven of nine years from 1991 to 1999. The population rate of change analysis supported that assertion because in seven of nine annual intervals from 1991 to 2000, λ -values were > 1 . Based on size-structure of Colorado pikeminnow in the Green River Basin, recruitment was low in all years of this study, 2000 to 2003. The population rate of change analysis also supported that assertion, because λ -values were < 1 , sometimes substantially so, in all years. Thus, size-structure metrics and the population rate of change analysis jointly support the thesis that reduced recruitment in recent years was a main factor in the apparent decline of Colorado pikeminnow abundance during the study period.

Some may also argue that the high recruitment years observed from 1992 to 1994 may be sufficient to maintain the population for many years. However, if one assumes an annual survival rate of 0.80 for fish recruited in those three high recruitment years, on average, only 21% of those

fish were alive in 2000, and only 11% in 2003. With only a single high recruitment year since 1994 (1998), it appears that recruitment events may need to be more frequent to forestall population declines of Colorado pikeminnow in the Green River.

A reason for low abundance of recruit-sized Colorado pikeminnow in 2000 to 2003 may be related to relatively low abundance of young-of-year produced in nursery areas (Fig. 20, Muth et al. 2000; McAda 2002; unpublished data Utah Division of Wildlife Resources). Density of age-0 Colorado pikeminnow in backwaters in autumn has declined rather dramatically since the early 1990's, especially in the middle Green River. Relatively strong year-classes in the middle and lower Green River were last produced in 1993. That year class would have first contributed adults to the Green River Colorado pikeminnow population in year 2000, the year when estimates of abundance of adult Colorado pikeminnow in the middle Green River were the highest observed during this study. This recruitment scenario was based on growth rates of Colorado pikeminnow presented by Osmundson et al. (1997), where an average age-0 fish in a given year-class (e.g., 1993) was expected grow to an average of 425 mm TL, a recruit-sized fish, six years later (Osmundson et al. 1997). That same group of fish would then recruit to adult size (≥ 450 mm TL) one year later at age 7 (e.g. year 2000). Subsequent year-classes (1994 to 1996) that would have contributed adults to the Green River population of Colorado pikeminnow from 2001 to 2003 were very weak in the middle Green River and only moderately strong or weak in the lower Green River.

In the Colorado River, strong recruitment year-classes of Colorado pikeminnow were also linked to strong year-classes of early life stages (Osmundson and Burnham 1998). The link between early life stage year-class strength and abundance of recruit-sized Colorado pikeminnow in the Green River Basin deserves further investigation. Such an analysis should include

information on production of larvae (Bestgen et al. 1998), abundance of juveniles in backwaters (Haines and Tyus 1990; Tyus and Haines 1991; Haines et al. 1998; McAda 2002), and biotic and abiotic factors that may influence year-class strength and recruitment to the adult size class (Bestgen 1996; Bestgen et al. 1997; Bestgen and Bundy 1998; Osmundson and Burnham 1998).

Probabilities of capture.--Relationships of capture probabilities and fish length suggested small and very large Colorado pikeminnow had very low probabilities of capture, which can, in part, be independent of abundance of that life stage. The linear term for capture probability as a function of TL indicated fish up to about 580-mm TL were progressively easier to capture, but the negative coefficient for the quadratic term forced the relationship to decline for large fish. We hypothesized that relatively small or very large fish may be more difficult to capture because of habitat use or behavioral differences. Small fish may occupy relatively shallow water or small backwaters, where accessibility by electrofishing boats is limited (Tyus and Haines 1991). Large fish may occupy particularly deep water where electrofishing is simply inefficient, or may be powerful enough to evade the electrofishing field when it is detected.

The only three Colorado pikeminnow captured during this study that were > 900-mm TL had not been previously tagged. A general expectation is that an adult Colorado pikeminnow captured in the Green River Basin has about a 50% probability of being tagged. Based on their size and presumed slow growth rates, those fish have likely been in the system long prior to 1991 (Osmundson et al. 1997). Sample size notwithstanding, the first capture of those large fish during this study (one died after release) was surprising given the level of sampling effort expended in previous sampling efforts (e.g., ISMP). Further, those and other large fish were never seen again in this study, despite relatively high levels of sampling effort, supported the notion that very large fish may be more elusive to capture techniques used here. However, we also believe

that low capture probabilities at the extremes of the length ranges observed here are biased low because the length terms in the quadratic equation attempt to fit the few data at the extremes. The result is steep downward trajectories of the tails of the distribution of probability of capture values that are forced to near zero, where estimates are also likely imprecise. It may be reasonable to truncate those distributions so marginal values do not approach zero, but criteria to do such were lacking. While it is conceivable that more small fish exist in the system than abundance estimates suggested, it is unrealistic to speculate that large numbers of very large and old individuals are going undetected by our sampling efforts. Thus, bias of abundance estimates for adult Colorado pikeminnow caused by low capture probabilities for large individuals is assumed negligible.

Transition rates.--Transition probabilities (ψ_i) reflected a general movement pattern of Colorado pikeminnow from the lower Green River and the Desolation-Gray Canyon reach upstream. This was not surprising given the abundance of relatively small Colorado pikeminnow in those reaches, including recruits, compared to other reaches. This pattern was also consistent with the Colorado River, where relatively small-bodied Colorado pikeminnow reared in lower sections of the river and eventually moved upstream as sub-adults or adults (Osmundson et al. 1998). Prevailing wisdom suggests that those mostly adult-sized fish would establish and maintain stable home ranges in most areas of the Green River Basin (e.g. Irving and Modde 2000). Perhaps drought or other conditions in some years, particularly 2002, forced fish to move from those relatively small streams such as the Yampa River to larger ones such as the middle Green River, a reach where net ψ_i was positive. However, we recommend against overinterpreting ψ_i 's presented here, given that most are rather imprecise and likely represent only a few fish.

Given larger sample sizes, it would be useful to compare ψ_i 's observed in this study to past or future estimates and relate these to environmental factors. Such an analysis would give greater insights into the basinwide dynamics of fish movement and would allow a more robust evaluation of the interplay of individuals among population segments. One useful comparison may be if Colorado pikeminnow use regulated and unregulated stream segments such as Lodore Canyon in the Green River differently under different hydrologic conditions (Bestgen and Crist 2000; Kitcheyan and Montagne 2005). Additional empirical analysis of growth and movements of Colorado pikeminnow, based on tag recaptures would also be useful to further understanding of the ecology of Colorado pikeminnow in the Green River Basin, as was demonstrated by Osmundson et al. (1997; 1998).

Analysis of transition rates may also be useful to understand the ecology of other fishes in the Green River Basin. For example, historical and ongoing investigations into the distribution, abundance, and movement patterns of northern pike in the Yampa River, Colorado, have yielded a substantial number of tag recaptures (Nesler 1995). Analysis of those tag recapture data, and estimation of ψ 's to determine whether northern pike in the Yampa River move from upstream source reaches, may aid management of Colorado pikeminnow that occupy critical habitat in downstream reaches.

CONCLUSIONS

- The sampling design fulfilled assumptions of the estimating model sufficiently well. The level of sampling effort and numbers of fish captured supported a relatively realistic estimating model that was useful to obtain relatively reliable abundance estimates and other demographic parameters for Colorado pikeminnow in the Green River Basin. Higher

probabilities of capture may be needed in river reaches with relatively small populations of Colorado pikeminnow if more precise estimates are desired.

- Capture-recapture sampling conducted in sections of the Green River Basin from 2000 to 2003 suggested a decline in abundance of Colorado pikeminnow in the Green River Basin, Colorado and Utah, over the study period. Based on the trend in annual point estimates, reductions were most severe in the middle Green River and the White River. Those reaches supported the highest number of Colorado pikeminnow in the Green River Basin. Reductions in abundance were less severe in the Yampa, Desolation-Gray Canyon, and lower Green River reaches. Significance of trends in point estimates were based on comparison of confidence limits for pairs of years, regression analysis to investigate the strength of trends of point estimates over time, the relative precision of point estimates, and our perception of the biological importance of the trends observed.

- Survival rates for adult Colorado pikeminnow from 2000 to 2003 were lower than survival rates estimated from ISMP data collected from 1991 to 1999. This suggested that apparent declines in abundance of adult Colorado pikeminnow in 2000 to 2003 were caused, in part, by lower survival rates.

- There was no support for the hypothesis that reduced survival of adult Colorado pikeminnow was due to sampling mortality.

- Abundance of recruit-sized fish during 2000 to 2003 sampling in the Green River Basin was lower than from ISMP sampling from 1991 to 1999. Recruitment rates may be less than mortality rates of adults during the study period. This suggested that apparent declines in abundance of adult Colorado pikeminnow in the Green River Basin in 2000 to 2003 were caused, in part, by lower recruitment rates.

- Reduced abundance of recruit-sized Colorado pikeminnow noted during this study may be due to weak year-classes of age-0 Colorado pikeminnow in the past several years in nursery areas of the middle and lower Green River. Trends in abundance of age-0 Colorado pikeminnow were from ISMP investigations that sampled backwaters of the Green River in autumn since 1986.

- The population rate of change analysis showed a trend similar to that for ISMP sampling from 1991 to 2003 and thus, was useful to track the trajectory of the population of adult Colorado pikeminnow in the Green River Basin. Because this type of analysis requires consistent sampling of the same locations from one year to the next, and can be accomplished with data collected from only a single sampling pass, this analysis may be useful to document trends of Colorado pikeminnow in the Green River Basin in years when the relatively intensive abundance estimation sampling is not conducted.

- The ISMP catch/effort data showed a reasonably close and proportional relationship with abundance estimates.

- Apparent reductions in abundance of adult and recruit-sized Colorado pikeminnow in the Green River Basin may be related to low, drought-related base flows that began about the same time this investigation began. The precise mechanism for the apparent reduction in Colorado pikeminnow abundance and low flows is unknown.

RECOMMENDATIONS

- Continue with the sampling protocol for Colorado pikeminnow in the Green River Basin as called for in the Recovery Goals.

- Increase sampling effort during the next abundance estimation sampling period to areas where no sampling occurred in 2000 to 2003, if low and access conditions permit (e.g., Green River between Tusher Wash Diversion downstream to Green River State Park, others).

- Investigate the need for, and the means to obtain, higher probabilities of capture of Colorado pikeminnow in reaches where abundance estimates were relatively imprecise. This may include addition of other gears such as fyke nets, or more sampling passes.

- Investigate the efficacy and advantages of data collection to continue ISMP-type sampling for catch-effort trends and to conduct the population rate of change analysis in years when intensive abundance estimation sampling is not conducted. Benefits of such sampling will need to be balanced against the potential negative effects of additional sampling on fish.

- Conduct an empirical analysis of growth and movements of Colorado pikeminnow, based on tag recaptures, to further understanding of the ecology of Colorado pikeminnow in the Green River Basin.

- Investigate the link between abundance dynamics of early life stages of Colorado pikeminnow and recruitment to later life stages. An understanding of effects of habitat, stream flow, and non-native fishes on recruitment would be especially useful.

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Table 1. Capture histories for Colorado pikeminnow captured in the period 2000 to 2003 in the Green River Basin, Colorado and Utah. The capture history digits represent whether an individual fish was captured in sampling years from 2000 to 2003, from left to right respectively, where a 1 denotes that an individual was captured that year and a 0 indicates that an individual was not captured. For example, a capture history of 0110 indicates that an individual was not captured in 2000, was captured in 2001 and 2002, but was not in 2003; there were 107 such individuals with that capture history in this study. A 1 indicates a capture in that year regardless of how many times it was recaptured among sampling passes within that year (e.g., no attempt was made to enumerate capture frequencies within years). Subtotals represent the number of fish captured exactly once, twice, three, or four times regardless of when it was captured

Capture history	Frequency	Percent
1000	1122	29.5
0100	1104	29.1
0010	452	11.9
0001	534	14.1
subtotal	3212	84.5
1100	212	5.6
1010	43	1.1
1001	43	1.1
0110	107	2.8
0101	66	1.7
0011	61	1.6
subtotal	532	14.0
1110	22	0.6
1101	15	0.4
1011	5	0.1
0111	6	0.2
subtotal	48	1.3
1111	8	0.2
subtotal	8	0.2
total	3800	100.0

Table 2. Huggins models to estimate abundance (derived from model parameters), survival (S), probability of capture (p) or recapture (c), and transition rate (ψ , or ψ) among reaches for Colorado pikeminnow in the Green River Basin, 2000 to 2003. Covariates include river reach (reach), sampling year or pass (year or pass), and fish total length (TL, plus the maximum polynomial terms indicated by the carat sign and a numeral where 2 = quadratic and 3 = cubic terms). The Additive effect in model 4 is a term to test for differences among capture and recapture rates; $S(\cdot)$ indicates a constant survival rate over all years with no covariates.

Models	AIC _c	Δ AIC _c	W	L	N	Deviance
1. $S(TL^3) \psi(reach+TL) p(reach*year*pass+TL^2)=c(reach*year*pass+TL^2)$	12926.41	0.00	0.35	1.00	81	12760.75
2. $S(TL^3) \psi(reach+TL) p(reach*year*pass+TL^3)=c(reach*year*pass+TL^3)$	12927.20	0.79	0.24	0.67	82	12759.44
3. $S(year+TL^3) \psi(reach+TL) p(reach*year*pass+TL^2)=c(reach*year*pass+TL^2)$	12928.09	1.68	0.15	0.43	83	12758.24
4. $S(TL^3) \psi(reach+TL) p(reach*year*pass+TL^2)=c(reach*year*pass+TL^2)+Additive$	12928.47	2.06	0.12	0.36	82	12760.71
5. $S(TL^2) \psi(reach+TL) p(reach*year*pass+TL^2)=c(reach*year*pass+TL^2)$	12929.82	3.41	0.06	0.18	80	12766.24
6. $S(\cdot) \psi(reach+TL) p(reach*year*pass+TL^2)=c(reach*year*pass+TL^2)$	12930.25	3.84	0.05	0.15	78	12770.86
7. $S(TL^3) \psi(reach) p(reach*year*pass+TL^2)=c(reach*year*pass+TL^2)$	12931.82	5.42	0.02	0.07	80	12768.25
8. $S(TL^3) \psi(reach+TL) p(reach*year*pass)=c(reach*year*pass)$	12940.20	13.79	0.00	0.00	79	12793.31
9. $S(\cdot) \psi(reach) p(reach*year*pass)=c(reach*year*pass)$	12989.48	63.07	0.00	0.00	75	12836.34
10. $S(year+TL) \psi(reach+TL) p(year*pass+TL)=c(year*pass+TL)$	13178.27	251.86	0.00	0.00	38	13101.46
11. $S(year+TL) \psi(reach+TL) p(reach+year*pass+TL)=c(reach+year*pass+TL)$	13180.71	254.30	0.00	0.00	42	13095.72

Table 3. Abundance estimates, 95% confidence limits, coefficients of variation (CV's, as %), and numbers of unique individuals captured (M_{t+1}) for adult (≥ 450 -mm TL) Colorado pikeminnow in the Yampa River, Colorado, 2000 to 2003.

Life						
stage	Year	Abundance	SE	95% CI	CV	M_{t+1}
<hr/>						
Adults						
	2000	317	105	184 - 623	33	82
	2001	320	48	245 - 438	15	120
	2002	277	87	157 - 512	31	33
	2003	224	75	123 - 434	34	31

Table 4. Abundance estimates, 95% confidence limits, coefficients of variation (CV's, as %), and numbers of unique individuals captured (M_{t+1}) for adult (≥ 450 -mm TL) and recruit-sized (400 to 449-mm TL) Colorado pikeminnow in the White River, Utah and Colorado, 2000 to 2003.

Life						
stage	Year	Abundance	SE	95% CI	CV	M_{t+1}
<hr/>						
Adults						
	2000	1100	220	767 - 1653	20	265
	2001	746	98	586 - 973	13	197
	2002	643	94	491 - 864	15	161
	2003	407	68	300 - 573	17	106
Recruits						
	2000	43	15	24 - 87	35	9
	2001	45	14	26 - 84	31	10
	2002	5	4	2 - 24	90	1
	2003	0	0	0 - 0		0

Table 5. Abundance estimates, 95% confidence limits, coefficients of variation (CV's, as %), and numbers of unique individuals captured (M_{t+1}) for adult (≥ 450 -mm TL) and recruit-sized (400 to 449-mm TL) Colorado pikeminnow in the Middle Green River, Utah, 2000 to 2003.

Life stage	Year	Abundance	SE	95% CI	CV	M_{t+1}
Adults						
	2000	1613	149	1359 - 1948	9	563
	2001	1184	115	986 - 1441	10	322
	2002	834	151	593 - 1192	18	97
	2003	663	107	491 - 918	16	143
Recruits						
	2000	107	20	76 - 158	19	30
	2001	133	26	93 - 199	20	29
	2002	22	15	7 - 78	70	2
	2003	43	16	22 - 91	38	7

Table 6. Abundance estimates, 95% confidence limits, coefficients of variation (CV's, as %), and numbers of unique individuals captured (M_{t+1}) for adult (≥ 450 -mm TL) and recruit-sized (400 to 449-mm TL) Colorado pikeminnow in the Desolation-Gray Canyon reach of the Green River, Utah, 2001 to 2003.

Life						
stage	Year	Abundance	SE	95% CI	CV	M_{t+1}
<hr/>						
Adults						
	2001	699	109	527 - 963	16	208
	2002	757	165	504 - 1166	22	99
	2003	621	129	423 - 942	21	100
Recruits						
	2001	163	33	114 - 247	20	42
	2002	72	28	36 - 154	39	8
	2003	152	44	90 - 269	29	20

Table 7. Abundance estimates, 95% confidence limits, coefficients of variation (CV's, as %), and numbers of unique individuals captured (M_{t+1}) for adult (≥ 450 -mm TL) and recruit-sized (400 to 449-mm TL) Colorado pikeminnow in the lower Green River, Utah, 2001 to 2003.

Life stage	Year	Abundance	SE	95% CI	CV	M_{t+1}
Adults						
	2001	355	56	270 - 496	16	143
	2002	261	51	184 - 388	19	65
	2003	227	49	154 - 352	22	54
Recruits						
	2001	71	16	48 - 116	23	24
	2002	31	13	16 - 69	41	6
	2003	89	27	53 - 162	30	16

Table 8. Probabilities of capture of Colorado pikeminnow from the Green River Basin 2000-2003, for each sampling occasion, reach, and year. Values were the maxima for quadratic relationships of probability of capture as a function of Colorado pikeminnow TL and TL² for each river reach and year, where relationships reached an asymptote for a fish about 540-mm TL. Estimates of p^* were from the Cormack-Jolly-Seber component of the model used to estimate annual survival rates (recaptures between years) and from the p 's for passes within years. Because p^* was estimated in that manner, we could calculate abundance estimates for the Yampa River in 2002 and 2003 where no animals were recaptured between passes within a single year.

River/reach	Sampling occasion	2000	2001	2002	2003	mean
Yampa River	1	0.047	0.165	0.045	0.014	0.068
	2	0.077	0.117	0.045	0.017	0.064
	3	0.173	0.171	0.045	0.076	0.116
	means	0.099	0.151	0.045	0.036	0.083
White River	1	0.101	0.104	0.110	0.103	0.104
	2	0.085	0.120	0.084	0.052	0.085
	3	0.110	0.082	0.122	0.064	0.094
	means	0.099	0.102	0.105	0.073	0.095
Middle Green River reach	1	0.086	0.050	0.045	0.037	0.054
	2	0.113	0.067	0.052	0.060	0.073
	3	0.197	0.179	0.035	0.078	0.122
	means	0.132	0.099	0.044	0.058	0.083
Desolation-Gray Canyon reach	1	NA	0.125	0.056	0.035	0.072
	2	NA	0.125	0.049	0.025	0.066
	3	NA	0.095	0.056	0.067	0.073
	means		0.115	0.053	0.042	0.070
Lower Green River reach	1	NA	0.087	0.089	0.048	0.075
	2	NA	0.109	0.125	0.056	0.096
	3	NA	0.274	0.088	0.087	0.150
	means		0.156	0.101	0.064	0.107
Overall mean		0.110	0.117	0.065	0.056	0.087

Table 9. Abundance estimates, 95% confidence limits, coefficients of variation (CV's, as %), and numbers of unique individuals captured (M_{t+1}) adult (≥ 450 -mm TL) and recruit-sized (400 to 449-mm TL) Colorado pikeminnow in the Green River Basin, Utah and Colorado, 2000 to 2003. The percent recruit values are the abundance of recruits/abundance of adult in the same year multiplied by 100. Year 2000 estimates include only the middle Green River reach and the White and Yampa rivers; estimates from 2001 to 2003 include those areas and the Desolation-Gray Canyon and lower Green River reaches.

Life stage	Year	Abundance	SE	95% CI	CV	M_{t+1}	% Recruits
Adults							
	2000	3030	286.8	2467 - 3592	9	910	
	2001	3303	206.1	2900 - 3707	6	990	
	2002	2771	282.7	2216 - 3325	10	455	
	2003	2142	232.7	1686 - 2598	11	434	
Recruits							
	2000	150	26.3	98 - 201	18	39	4.9
	2001	412	51.1	312 - 512	12	105	12.5
	2002	130	35.5	61 - 200	27	17	4.7
	2003	284	55.8	175 - 393	20	43	13.3

* Year 2000 estimates include only the middle Green River reach and the Yampa and White rivers.

Table 10.—Apparent survival probability estimates (S , 95% CI) from capture-recapture data for sub-adult and adult Colorado pikeminnow captured in the Green River Basin in two periods, 1991-1999 and 2000 to 2003. Data for the intervals 1991-1999 were collected during a standardized monitoring program to estimate catch/effort indices for Colorado pikeminnow and were from about 23% of occupied habitat in the Green River Basin. Annual interval data from 2000-2003 were collected during a study to estimate abundance of adult and sub-adult Colorado pikeminnow throughout the Green River Basin; 2000-2001 data were from only the middle Green, Yampa, and White rivers. Estimates of probabilities of capture (p) for Colorado pikeminnow for the two time periods are also presented.

Parameter	Period	S or p	95% CI
Survival	1991-1999	0.82	0.709 to 0.891
	2000-2003	0.65	0.586 to 0.708
Probability of capture	1991-1999	0.053	0.038 to 0.074
	2000-2003	0.090	0.054 to 0.119

Table 11. Annual transition probabilities (ψ_{ij} , movement to a different reach between years) for the average-sized Colorado pikeminnow (500.4-mm TL) captured in the Green River Basin, Utah and Colorado, 2000 to 20003. River reaches are: Yampa R. = Yampa River (RK 192 to 74), White R. = White River (RK 167.4 to 0), middle Green R. = middle Green River reach (RK = 539.4 to 396.1), Deso-Gray = Desolation-Gray Canyon reach, Green River (RK 395.9 to 206.1), and lower Green R. = lower Green River reach (RK 193.2 to 0).

River reach	ψ	95% CI	
White R. to Yampa R.	0.007	0.001	to 0.055
White R. to middle Green R.	0.048	0.022	to 0.102
White R. to Deso-Gray	0.080	0.043	to 0.144
White R. to Lower Green R	0.003	0.000	to 0.067
Yampa R. to White R.	0		
Yampa R. to middle Green R.	0.036	0.009	to 0.135
Yampa R. to Deso-Gray	0.018	0.003	to 0.122
Yampa R. to lower Green R.	0		
middle Green R. to White R.	0.022	0.011	to 0.045
middle Green R. to Yampa R.	0.018	0.007	to 0.045
middle Green R. to Deso-Gray	0.045	0.024	to 0.081
middle Green R. to lower Green R.	0.001	0.000	to 0.115
Deso-Gray to White R.	0.032	0.010	to 0.099
Deso-Gray to Yampa R.	0		
Deso-Gray to middle Green R.	0.078	0.031	to 0.186
Deso-Gray to lower Green R.	0.041	0.012	to 0.131
lower Green R. to White R.	0		
lower Green R. to Yampa R.	0		
lower Green R. to middle Green R.	0		
lower Green R. to Deso-Gray	0.121	0.048	to 0.274

Table 12. Average annual transition probabilities (ψ , annual probability of movement to or from each reach, using only non-zero values) for the average-sized Colorado pikeminnow (499.5-mm TL) captured in the Green River Basin, Utah and Colorado, 2000 to 20003. A positive net ψ suggested more fish moved into the reach than out, a negative value of ψ suggested more fish moved out of the reach than into it. River reaches are: Yampa R. = Yampa River (RK 192 to 74), White R. = White River (RK 167.4 to 0), middle Green R. = middle Green River reach (RK = 539.4 to 396.1), Deso-Gray = Desolation-Gray Canyon reach, Green River (RK 395.9 to 206.1), and lower Green R. = lower Green River reach (RK 193.2 to 0).

River reach	Average ψ to:	Average ψ from:	Net ψ
Yampa River	0.012	0.027	-0.015
White River	0.027	0.035	-0.008
middle Green River	0.054	0.021	0.033
Desolation-Gray Canyon, Green River	0.066	0.050	0.016
lower Green River	0.015	0.121	-0.106

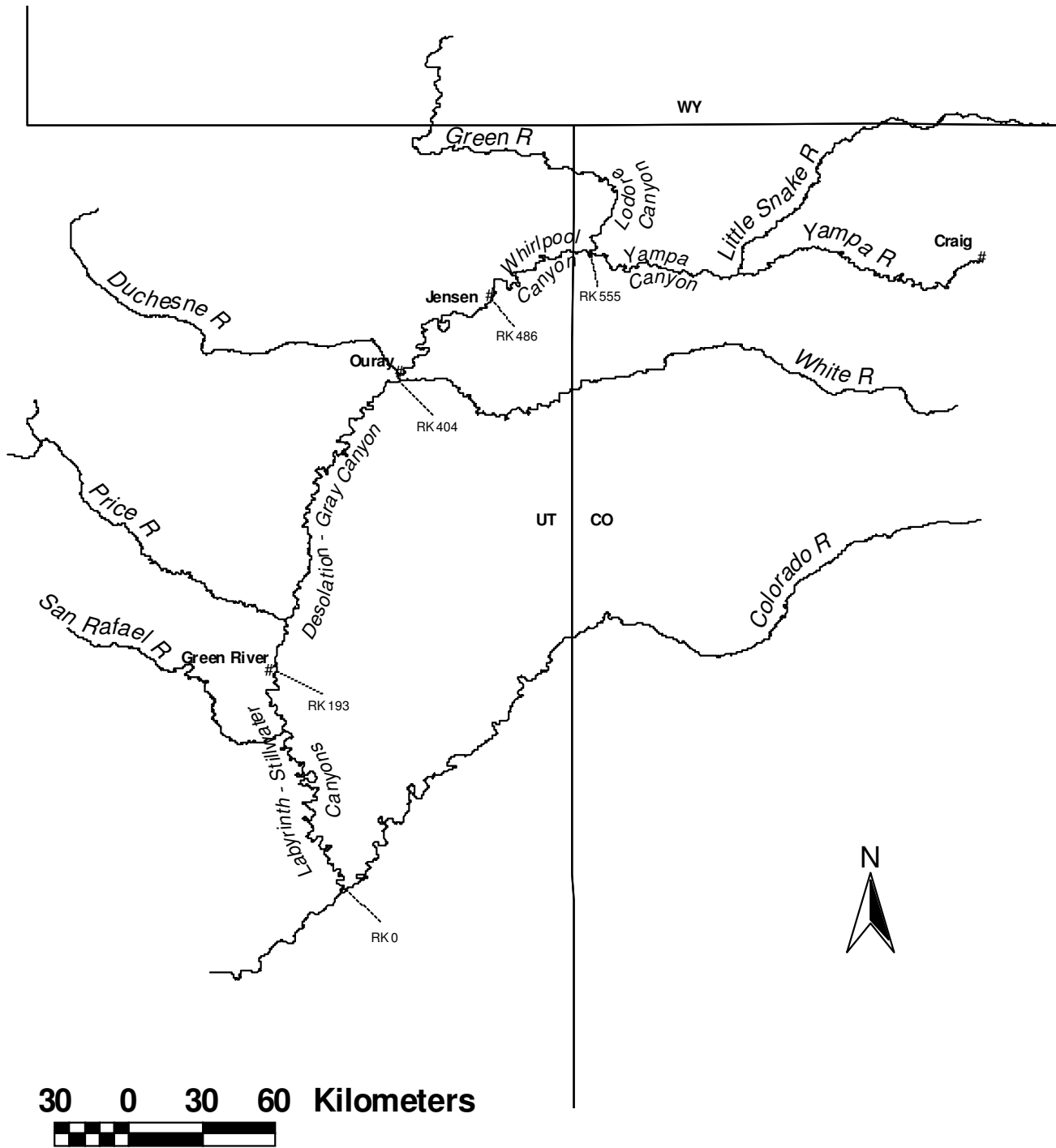


Figure 1. Map of Green River Basin study area.

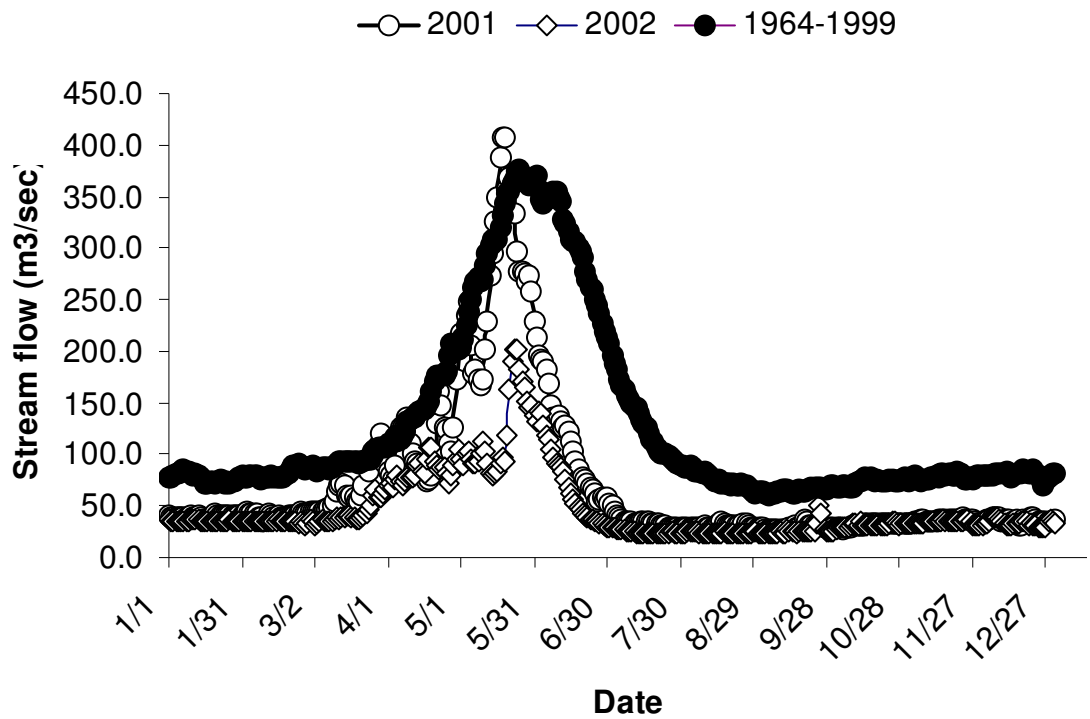


Figure 2. Average daily discharge of the Green River, near Jensen, Utah (gauge # 09261000), for the period 1964 to 1999, and in two study-period drought years, 2001 and 2002.

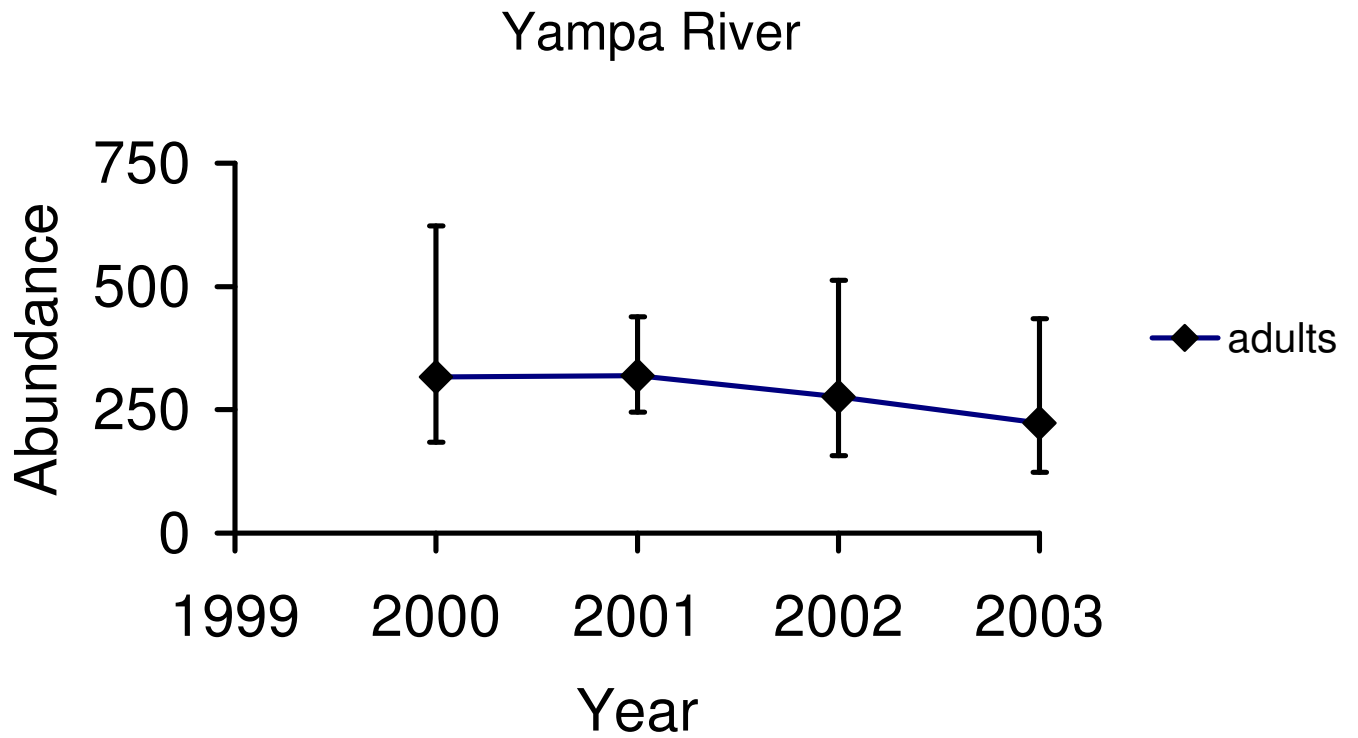


Figure 3. Abundance of Colorado pikeminnow adults (≥ 450 -mm TL) in the Yampa River, Colorado, 2000 to 2003. Error bars are 95% confidence limits.

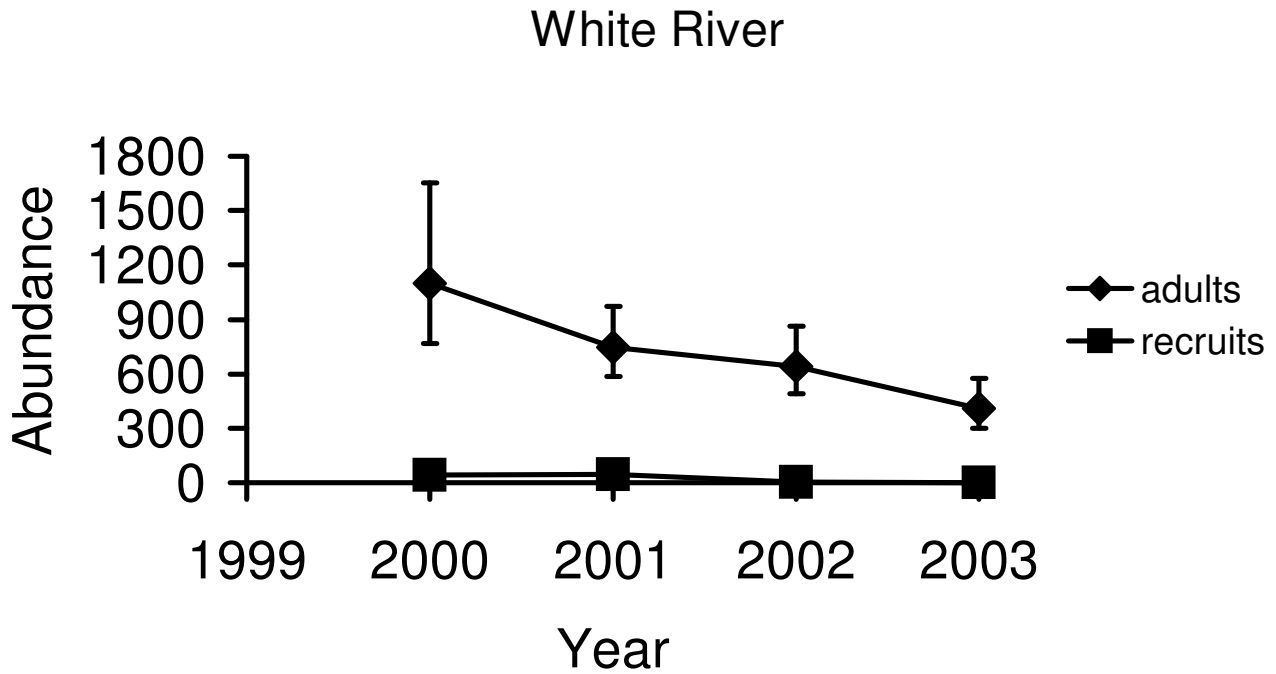


Figure 4. Abundance of Colorado pikeminnow adults (≥ 450 -mm TL) and recruits (400 to 449 mm TL) in the White River, Utah and Colorado, 2000 to 2003. Error bars are 95% confidence limits, which may be obscured by symbols for recruits.

Middle Green River

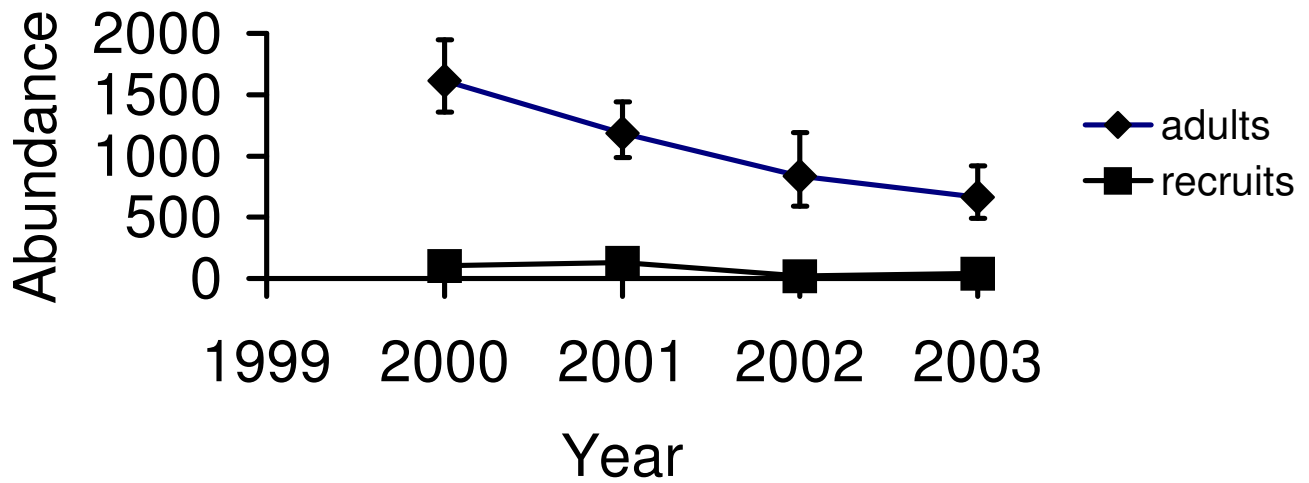


Figure 5. Abundance of Colorado pikeminnow adults (≥ 450 -mm TL) and recruits (400 to 449 mm TL) in the middle Green River, Utah, 2000 to 2003. Error bars are 95% confidence limits, which may be obscured by symbols for recruits.

Desolation-Gray Canyon, Green River

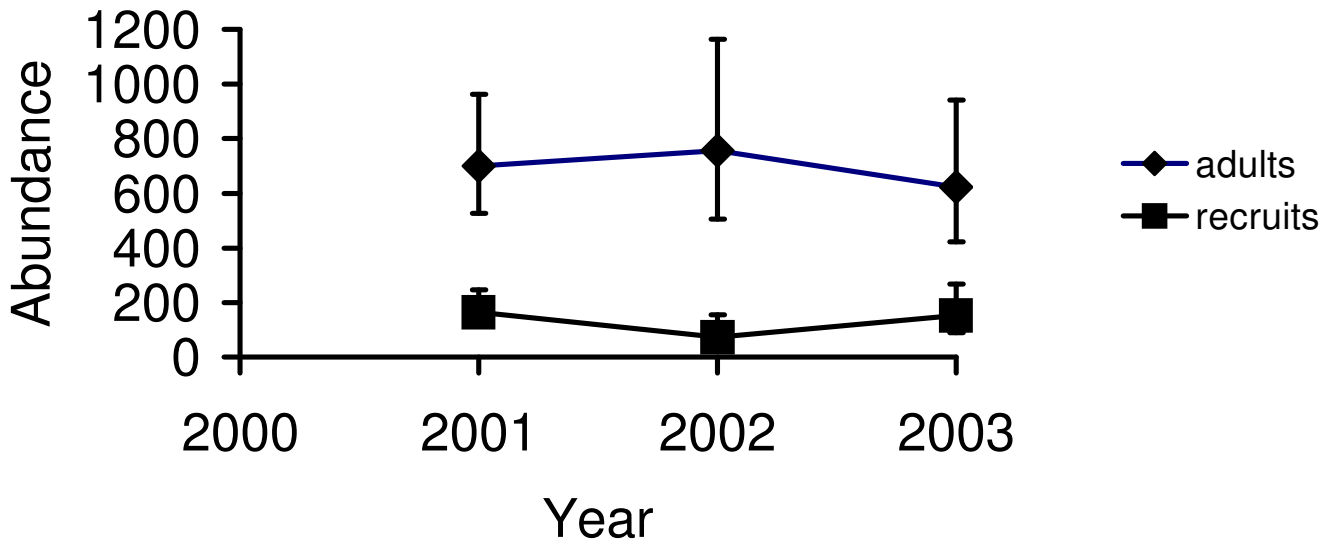


Figure 6. Abundance of Colorado pikeminnow adults (≥ 450 -mm TL) and recruits (400 to 449 mm TL) in the Desolation-Gray Canyon reach of the Green River, Utah, 2001 to 2003. Error bars are 95% confidence limits, which may be obscured by symbols for recruits.

Lower Green River

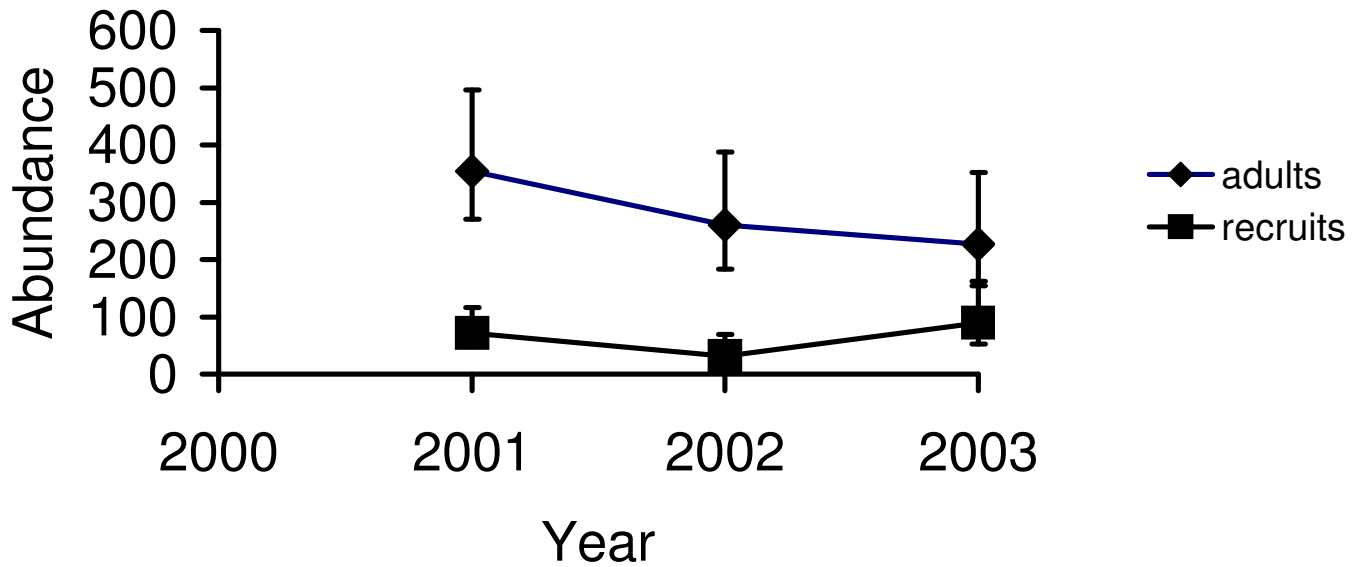


Figure 7. Abundance of Colorado pikeminnow adults (≥ 450 -mm TL) and recruits (400 to 449 mm TL) in the lower Green River, Utah, 2001 to 2003. Error bars are 95% confidence limits, which may be obscured by symbols for recruits.

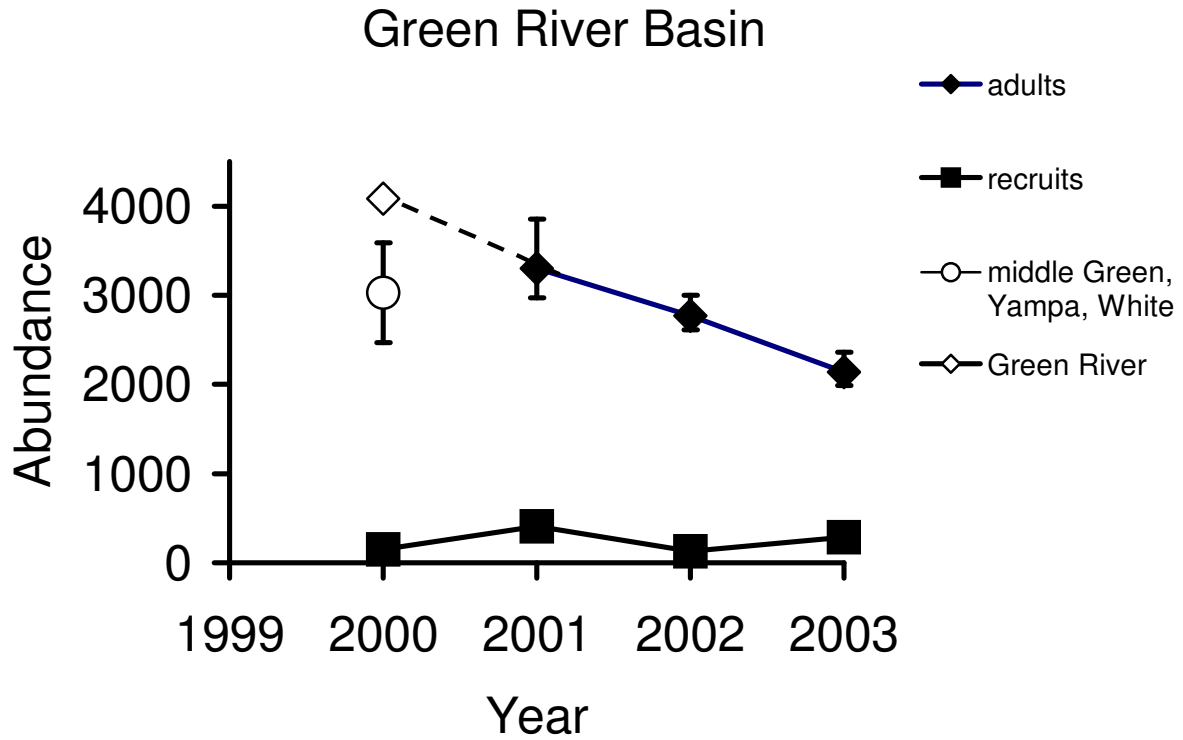


Figure 8. Abundance of Colorado pikeminnow adults (≥ 450 -mm TL) and recruits (400 to 449 mm TL) in the Green River Basin, Utah and Colorado, 2000 to 2003. Error bars are 95% confidence limits, which may be obscured by symbols for recruit. The year 2000 estimate is for the middle Green River reach, and the White and Yampa rivers only.

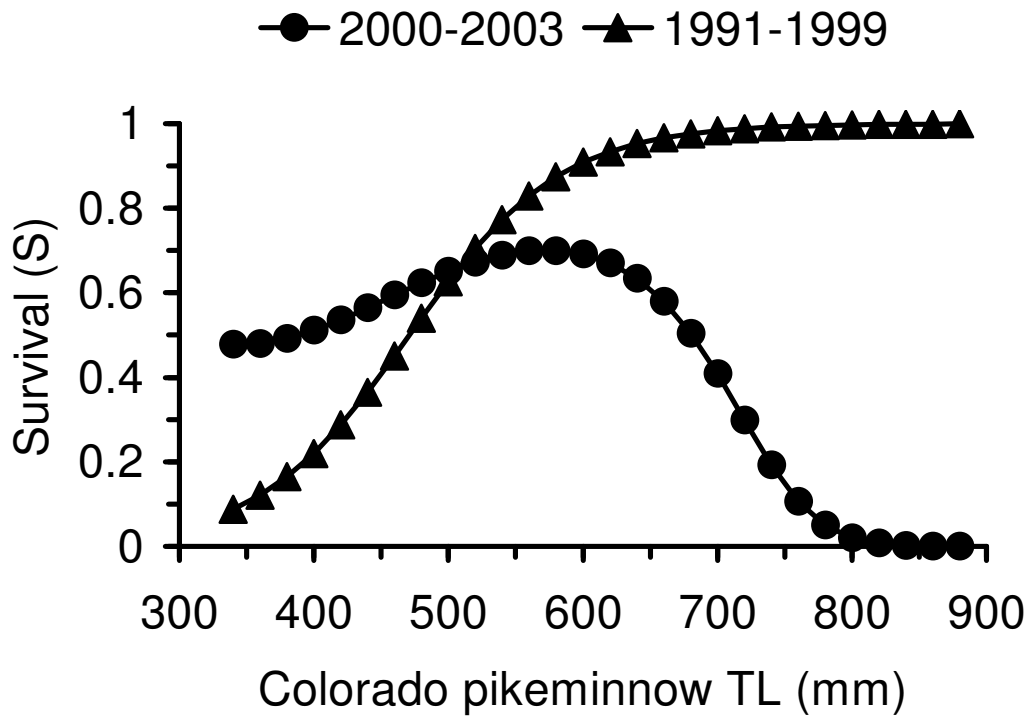


Figure 9. Survival of Colorado pikeminnow as a function of TL (mm) in the Green River Basin from 1991 to 1999 and 2000 to 2003. The 1991-1999 data were collected during Interagency Standardized Monitoring Program sampling, data from other periods were during abundance estimation sampling.

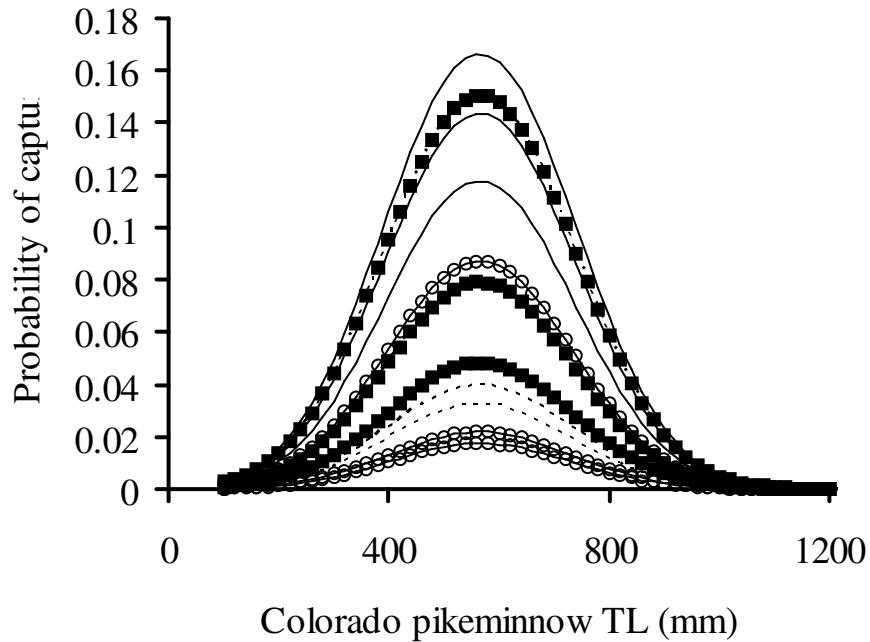


Figure 10. Probability of capture of Colorado pikeminnow as a function of length for sampling passes (only years identified) conducted in the Yampa River, Colorado, 2000 to 2003. Year 2000 passes are the dashed lines with solid squares, 2001 passes are the solid lines, year 2002 passes are those with a dashed line (the lowermost two passes overlap completely), and 2003 passes are those with a solid line and open circle symbols.

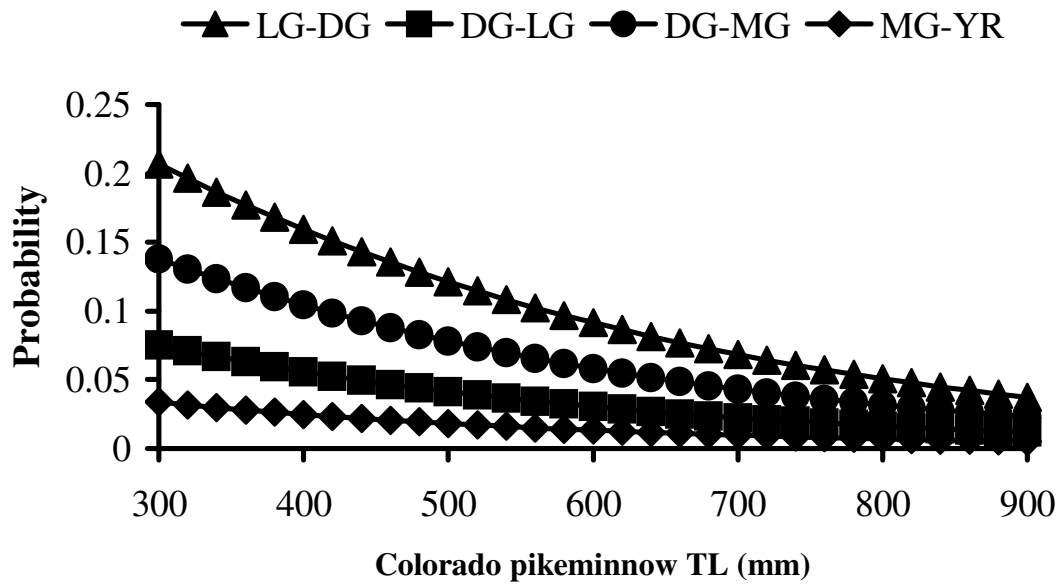


Figure 11. Transition probabilities (ψ) for Colorado pikeminnow of different lengths for various reach combinations in the Green River Basin, Utah and Colorado, 2000 to 2003. LG = lower Green River reach, DG = Desolation-Gray Canyon reach of the Green River, MG = middle Green River reach, and YR = Yampa River.

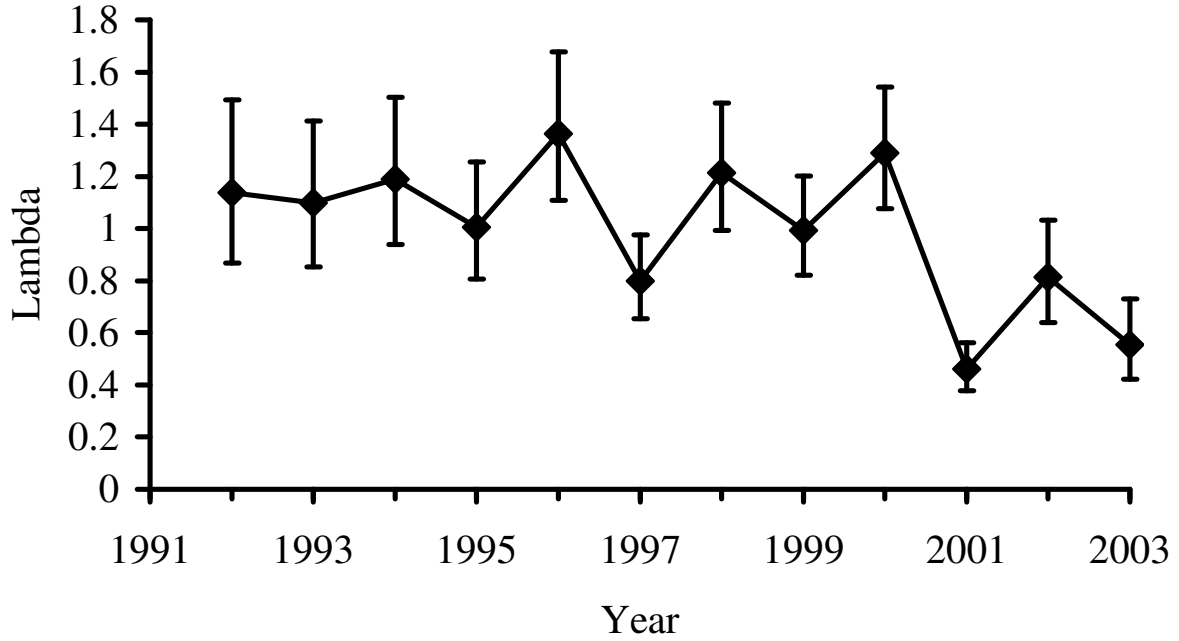


Figure 12. Estimated finite rate of population change (λ_i) for ISMP data collected in the Green River Basin, Utah and Colorado, at 10 sites from 1991 to 2003. Error bars are 95% confidence limits, $\lambda > 1$ represents an expanding population, $\lambda < 1$ represents a declining population, $\lambda = 1$ represents a stable population.

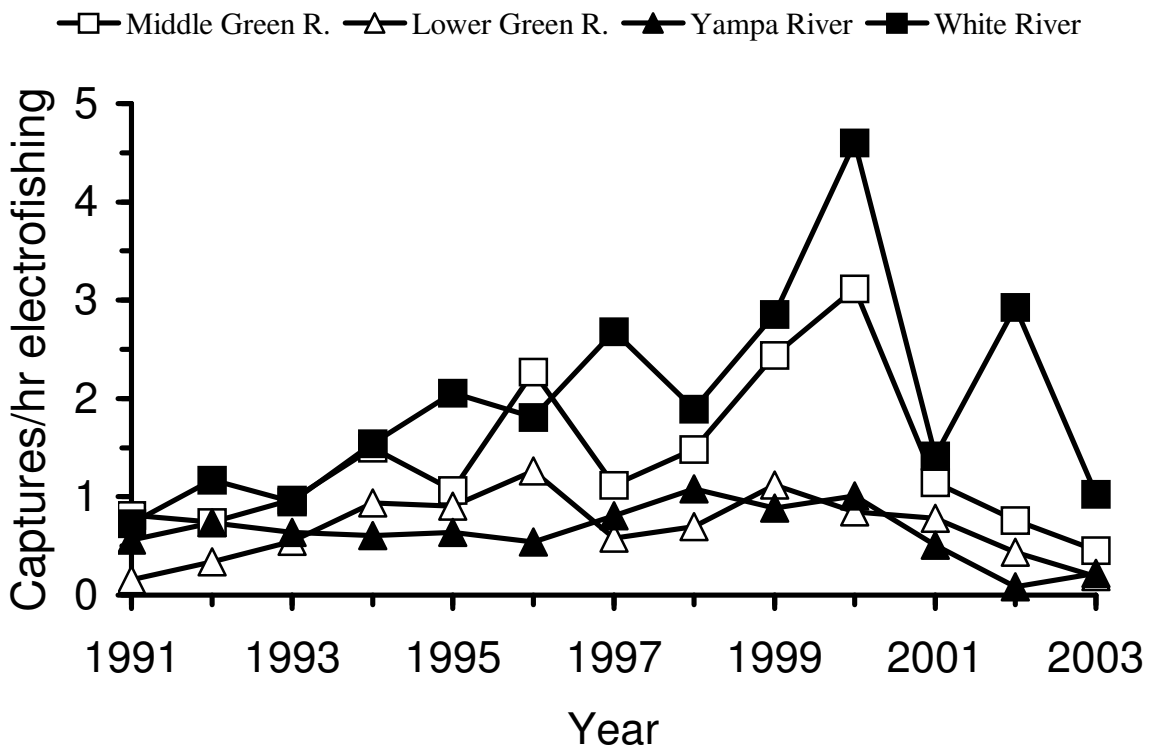


Figure 13. Interagency standardized monitoring program (ISMP) captures of sub-adult and adult Colorado pikeminnow per hour of electrofishing effort in the Green River Basin, 1991 to 2003.

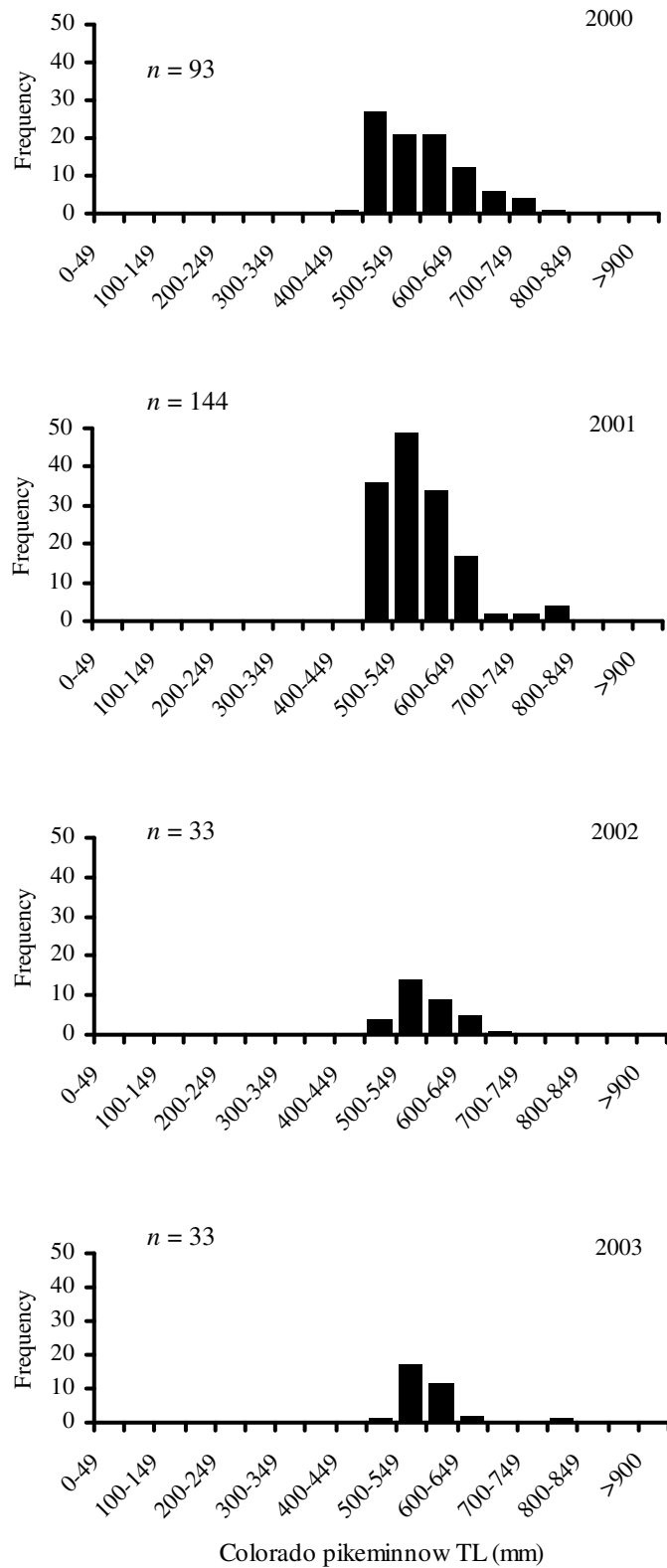


Figure 14. Length-frequency histograms for Colorado pikeminnow captured in the Yampa River, Colorado, 2000 to 2003, during Green River Basin abundance estimation sampling.

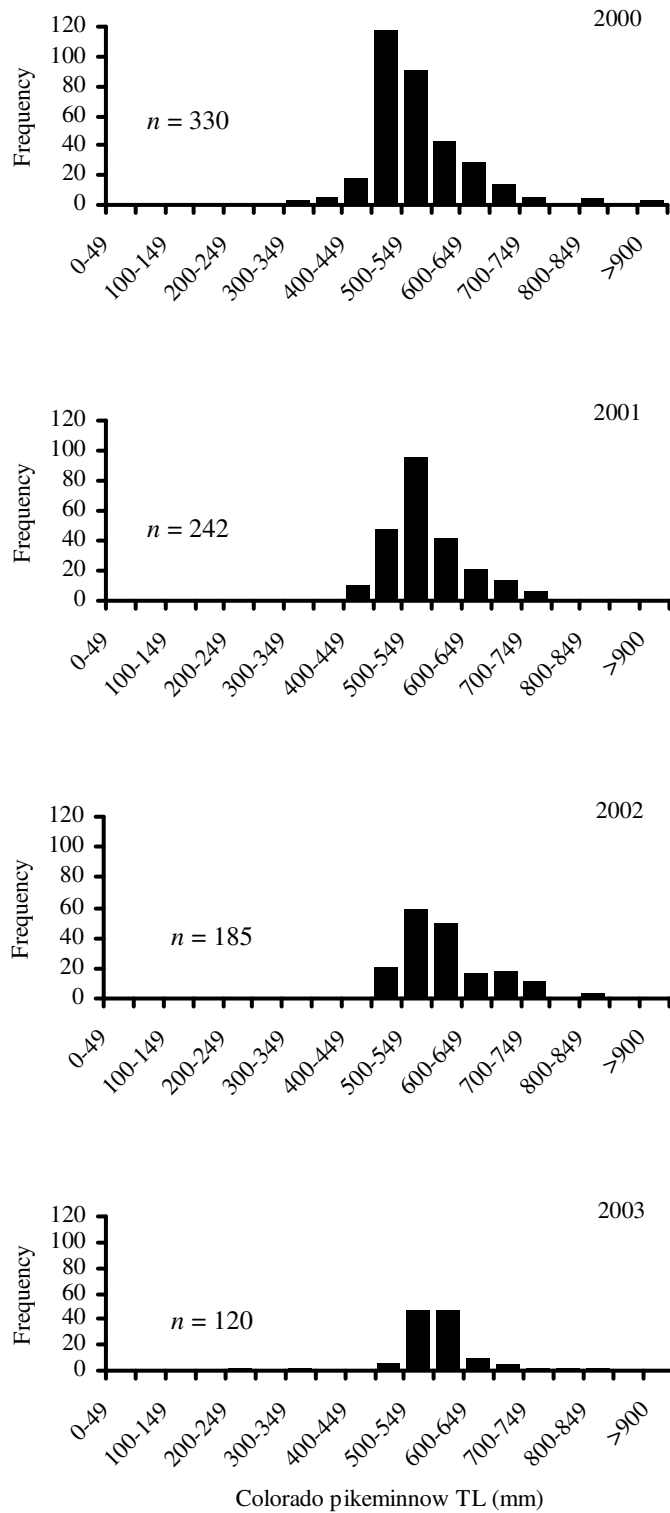


Figure 15. Length-frequency histograms for Colorado pikeminnow captured in the White River, Colorado, 2000 to 2003, during Green River abundance estimation sampling.

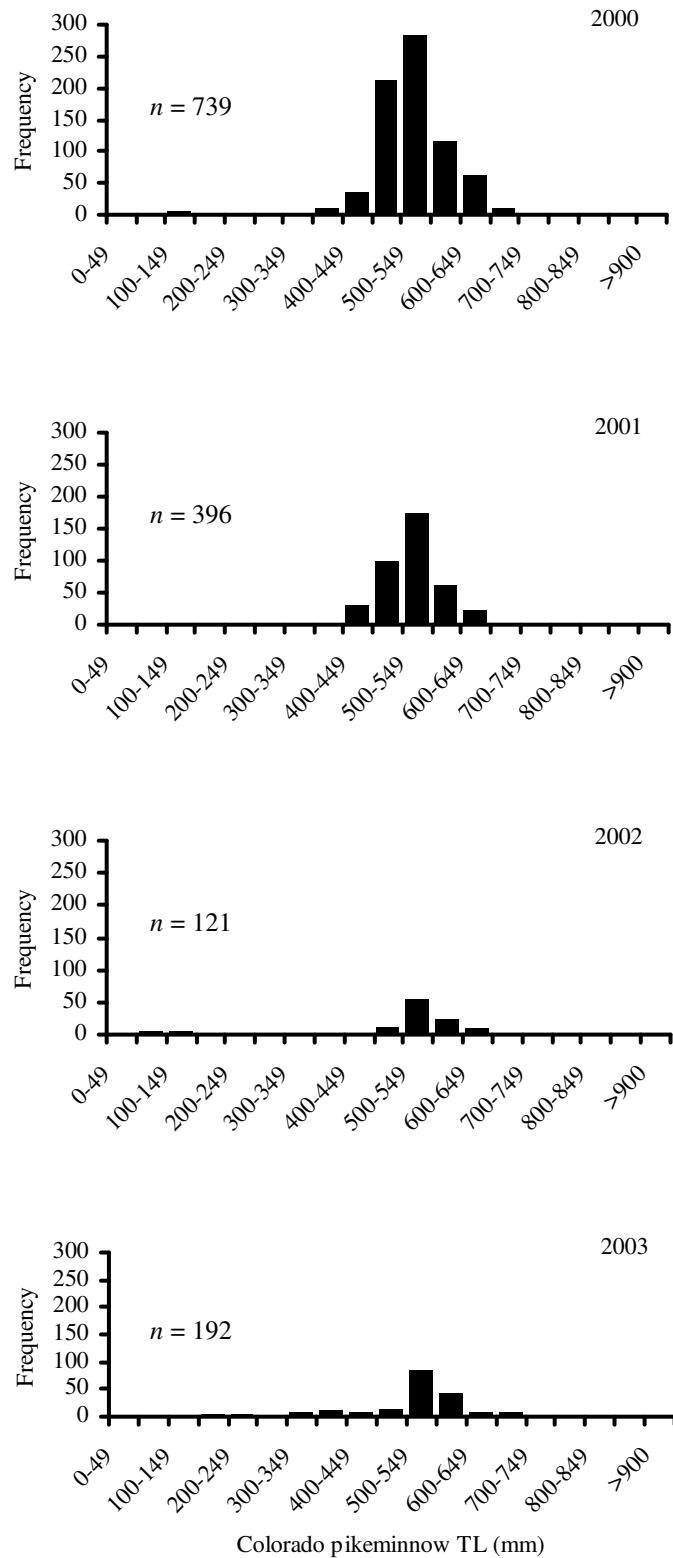


Figure 16. Length-frequency histograms for Colorado pikeminnow captured in the middle Green River, Utah, 2000 to 2003, during Green River abundance estimation sampling.

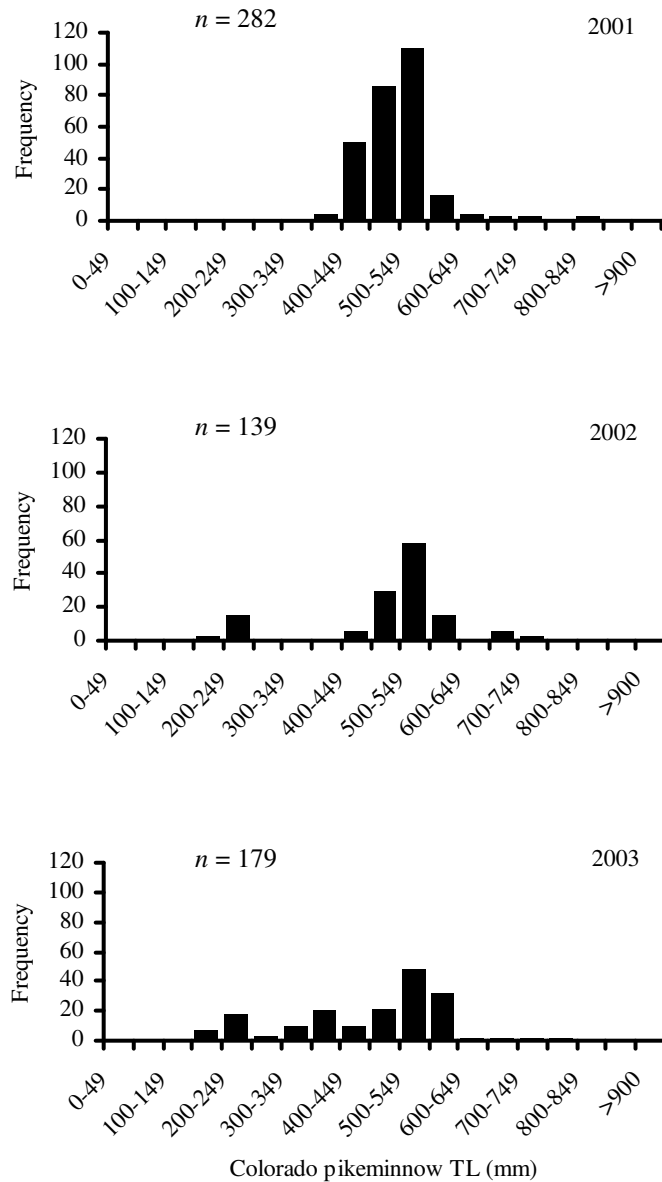


Figure 17. Length-frequency histograms for Colorado pikeminnow captured in the Desolation-Gray Canyon reach of the Green River, Utah, 2001 to 2003, during Green River abundance estimation sampling.

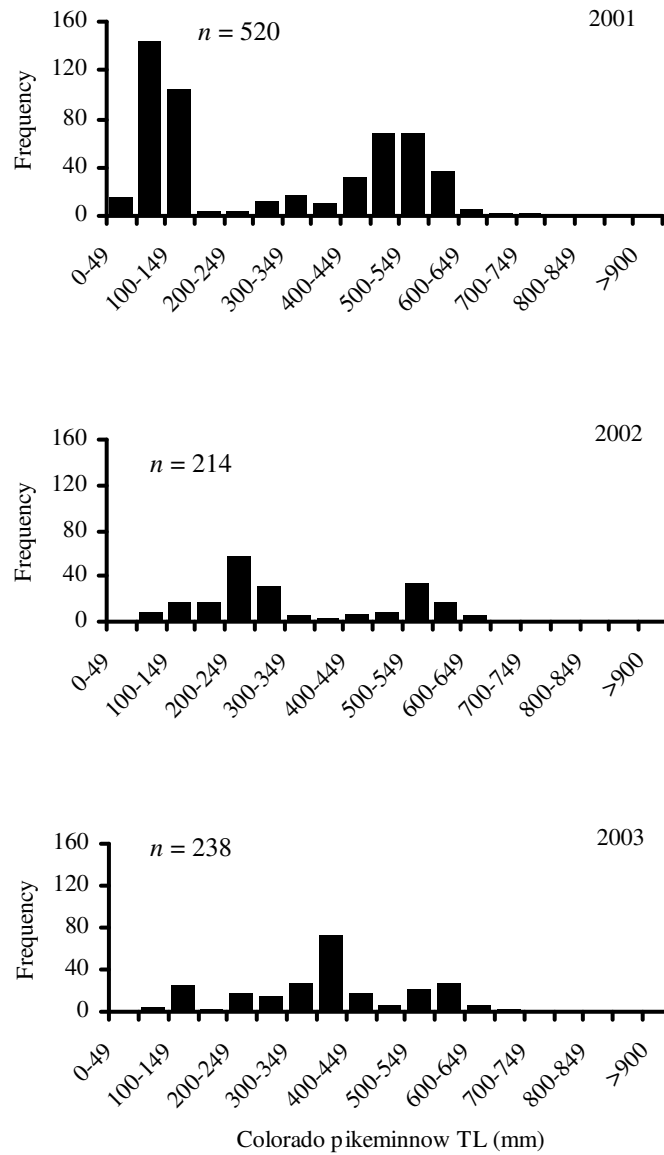


Figure 18. Length-frequency histograms for Colorado pikeminnow captured in the lower Green River reach, Utah, 2001 to 2003, during Green River abundance estimation sampling.

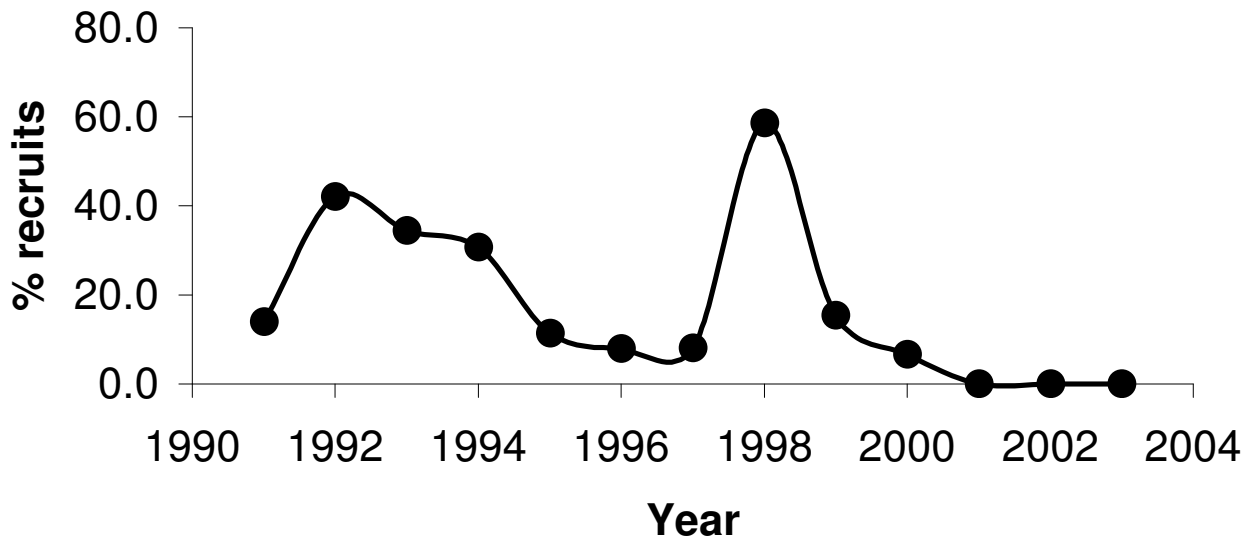


Fig. 19. Percentage of recruit-sized (400 to 449 mm TL) Colorado pikeminnow relative to the number of adults (≥ 450 mm TL) in Interagency Standardized Monitoring Program samples collected from the Green River Basin, Utah and Colorado, 1991 to 2003.

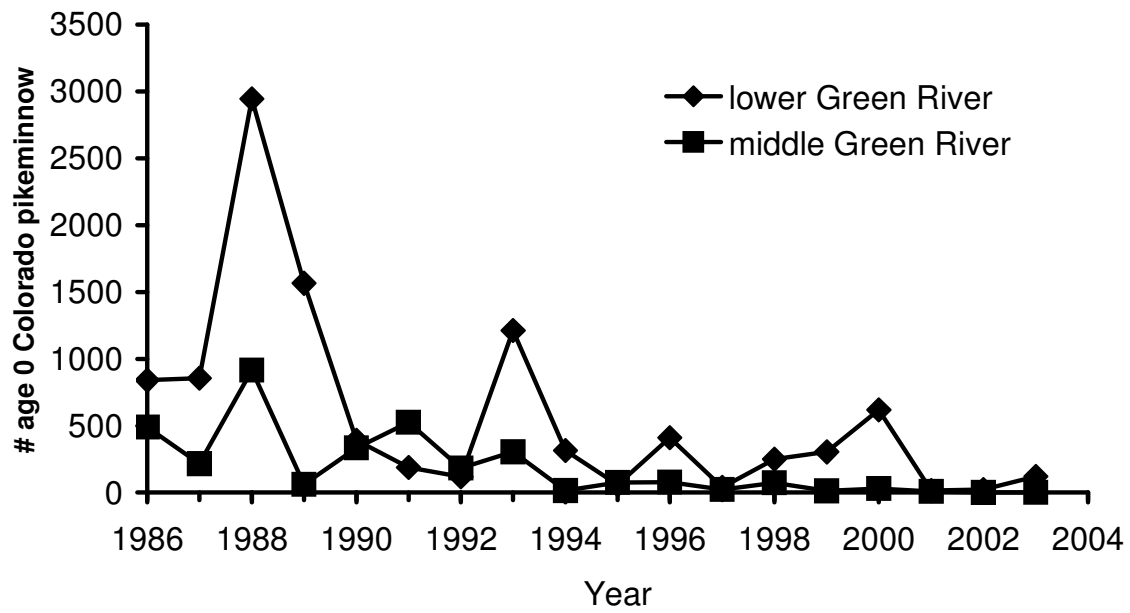


Figure 20. Abundance of age-0 Colorado pikeminnow in seine samples from backwaters in the middle and lower Green rivers, Utah, 1986 to 2003.

APPENDICES

Appendix I. Sampling dates, capture data, and effort for middle Green River abundance estimation sampling for Colorado pikeminnow, 2000.

	Dates	Days Sampled	River KM Sampled	Number of unique samples			Electrofishing Effort (hours)	Number of Pikeminnow Captured	Number of Pikeminnow Recaptured ¹
				Trammel/ Electro- fishing	Fyke Nets	Electro- fishing			
Green River									
Trip 1	April 11 - 27	10	535-412	4		10	42	176	45
Trip 2 (ISMP)	May 2 - 9	4	538-394			28	39	196	58
Trip 3	May 18- June	8	538-394	4		14	53	264	97
Trip 4	June 6- 16	7	538-396	1		12	43	102	54
Totals		29 days		9		64	177 hours	738	254
Yampa River									
Trip 1	April 18- 27	8	192-79	37		21	13	14	6
Trip 2	May 6- 14	9	192-79	14	12	23	15	23	8
Trip 3	May 22- June	11	192-79	30	18	18	18	48	24
Trip 4	June 20- 24	4	192-82		2	5	15	8	3
Totals		32 days		81	32	67	61 hours	93	41
White River									
Trip 1	April 18-28	5	163-39			18	50	61	10
Trip 1 (ISMP)	May 10	1	39-0			8	12	50	14
Trip 2	May 10-25	7	163-0			15	Not Available	92	21
Trip 3 (ISMP)	May 25-25	2	167-153			4	6	32	11
Trip 3	May 31 - June	7	147-0			11	58	85	35
Totals		22 days				56	127 hours	320	91

¹ Recaptured fish include those previously tagged at any time in the past including days earlier, on previous trips, or previous years.

Appendix II. Sampling dates, capture data, and effort for middle Green River abundance estimation sampling for Colorado pikeminnow, 2001.

	Dates	Days Sampl ed	River Miles Sampled	Total Effort (hours)			Number of Pikeminnow Captured ¹	Number of Pikeminnow Recaptured ²
				Trammel /Electro- fishing	Fyke Nets	Electro- fishing		
Green River								
Trip 1	April 16 - 24	9	535-412	0		45.41	64	
Trip 2	May 1 - 11	11	538-394	0.08		68.59	87	
Trip 3	May 14-May 24	11	538-394		7.15	80.53	158	
Trip 4	May 29 - June 6	9	538-396		7.25	58.52	85	
Totals		40		0.08	14.4	253.05	394	36
Yampa River								
Trip 1	April 24 - May 2	9	192-74	0.42		49.32	51	
Trip 2	May 11 - 19	9	192-74	1.07	87.23	45.69	36	
Trip 3	May 27- June 4	9	192-74	1.13	141.66	38.34	44	
Trip 4	June 12 - 19	8	192-74	0.33	50.41	40.85	9	
Totals		35		2.95	279.3	174.2	140	20
White River								
Trip 1	April 16-24	9	163-39			73.38	79	
Trip 2	May 8-23	16	163-0			61.75	94	
Trip 3	May 30- June 5	7	167-0			68.83	63	
Totals		22				203.96	236	24

¹ Total pikeminnow captured includes recaptures. ² Recaptured fish include those handled on previous sampling passes in 2001.

Appendix III. Sampling dates, capture data, and effort for middle Green River abundance estimation sampling for Colorado pikeminnow, 2002.

	Dates	Days Sampled	River Miles Sampled	Total Effort (hours)			Number of Pikeminnow Capture Events ¹
				Trammel/ Electro- fishing	Fyke Nets	Electro- fishing	
Green River							
Trip 1	April 30 – May 15	8	536-396	0	0	55	37
Trip 2	May 16 – 30	9	536-396	*	0	69	43
Trip 3	May 31 – June 10	7	536-396	0	0	56	29
Trip 4	July 11	1	525-514	0	0	3	1
Totals		35			0	182	110
Yampa River							
Trip 1	April 25 - May 3	8	192-72	0	0	46	11
Trip 2	May 11 – 19	8	196-72	0	0	52	11
Trip 3	May 26 - June 3	9	196-81	.19	0	57	9
Trip 4	June 12 – 16	5	192-140	0	0	10	2
Totals		30		.19	0	166	33
White River							
Trip 1	April 15 – 23	5	167-0	0	0	61	64
Trip 2	April 26 – May 3	5	167-0	0	0	64	49
Trip 3	May 8 - 24	9	167-0	0	0	53	72
Totals		19				178	185

¹ Total Number of pikeminnow captured including recaptures. * Effort not recorded.

Appendix IV. Sampling dates, capture data, and effort for middle Green River abundance estimation sampling for Colorado pikeminnow, 2003. All fish reported are 450 mm TL or greater.

	Dates	Days Sampled	River Miles Sampled	Total Effort (hours)			Number of Pikeminnow Capture Events ¹
				Trammel/ Electro- fishing	Fyke Nets	Electro- fishing	
Green River							
Trip 1	April 22 – May 12	10	538-396	0	0	67	38
Trip 2	May 13 – 27	10	538-396	0	0	65	54
Trip 3	May 28 – June 13	11	538-396	0	0	62	63
Totals		31		0	0	194	155
Yampa River							
Trip 1	April 24 - May 3	9	192-79	.54	124	41	4
Trip 2	May 12 – 20	8	192-79	.92	106	57	5
Trip 3	May 28 - June 14	9	192-71	3.85	342	52	22
Trip 4	June 15 – 25	9	192-71	.90	151	68	2
Totals		35		6.21	723	218	33
White River							
Trip 1	April 21 – 30	8	167-0	0	0	63	56
Trip 2	April 29 – May 15	7	167-0	0	0	53	27
Trip 3	May 5 - 29	8	167-0	0	0	61	36
Totals		23				177	119

¹ Total number of pikeminnow captured including recaptures.

Appendix V. Sampling dates, capture data, and effort for lower Green River abundance estimation sampling for Colorado pikeminnow, 2001.

Dates	Days Sampl ed	River Miles Sampled	Total Effort (hours)			Number of Pikeminnow Captured ¹	Number of Pikeminnow Recaptured ²
			Trammel/ Electro- fishing	Fyke Nets	Electro- fishing		
Deso-Gray							
Trip 1	March 26 - Apr 9	14	390 - 193		91.2	105	
Trip 2	April 17 - May 2	16	390 - 193		n/a ³	102	
Trip 3	May 7 - 16	10	390 - 193		69.7	75	
Totals		40				282	26
Lower Green							
Trip 1	March 12 - 21	10	193 - 0		78.18	43	
Trip 2	April 1 - 11	11	193 - 0		81.62	36	
Trip 3	April 21- May 2	12	193 - 0		81.74	57	
Trip 4	May 20 - 30	11	193 - 0		76.27	102	
Totals		44			317.81	238	28

¹ Total number of pikeminnow captured includes recaptures.

² Recaptured fish include those handled on previous sampling passes in 2001.

³ Effort meter on electrofisher not working.

Appendix VI. Sampling dates, capture data, and effort for lower Green River abundance estimation sampling for Colorado pikeminnow, 2002.

	Dates	Days Sampled	River Miles Sampled	Total Effort (hours)			Number of Pikeminnow Captured ¹
				Trammel /Electro- fishing	Fyke Nets	Electro- fishing	
Deso-Gray							
Trip 1	March 23 - Apr 11	9	396 - 208	0	0	81	47
Trip 2	April 20 - May 7	7	396 - 208	0	0	80	41
Trip 3	May 11 - May 17	7	396 -208	0	0	69	49
Totals		23				230	137
Lower Green							
Trip 1	April 7 - 17	9	193 - 2	0	0	86	59
Trip 2	April 21 - May 1	9	193 - 2	0	0	88	95
Trip 3	May 5 - May 15	9	193 - 2	0	0	73	61
Totals		27 days				247	215

¹ Total number of Colorado pikeminnow captured includes recaptures.

Appendix VII. Sampling dates, capture data, and effort for lower Green River abundance estimation sampling for Colorado pikeminnow, 2003.

Dates	Days Sampled	River Miles Sampled	Total Effort (hours)			Number of Pikeminnow Captured ¹	
			Trammel/ Electro- fishing	Fyke Nets	Electro- fishing		
Deso-Gray							
Trip 1	March 24- April 2	8	396 - 206	0	0	57	33
Trip 2	April 14 - April 23	8	396 - 206	0	0	53	22
Trip 3	May 5 - May 14	7	396 -206	0	0	48	21
Trip 4	June 2 - June 6	5	396 - 206	0	0	65	41*
Total		28		0	0	223	117
Lower Green							
Trip 1	April 13 - April 23	9	193 - 0	0	0	91	16
Trip 2	May 6 - May 16	9	193 - 0	0	0	84	14
Trip 3	May 25 - June 4	9	193 - 0	0	0	78	29
Total		27		0	0	253	59

¹ Total number of Colorado pikeminnow (over 450-mm TL) captured includes recaptures.

* Includes ten Colorado pikeminnow assumed to be adult size for which no length data was available (lost data sheets).