Population Dynamics of Colorado Pikeminnow in the Upper Colorado River

Final Report

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EXECUTIVE SUMMARY

Dynamics of the Colorado River population of Colorado pikeminnow *Ptychocheilus lucius*, an endangered fish species endemic to the Colorado River basin, were investigated from 1991 to 2000. Two multi-year data collection efforts were made: the first, from 1991 to 1994, and the second, from 1998 to 2000. Primary objectives included capturing and marking Colorado pikeminnow from throughout the study area, developing population estimates from the resulting mark-recapture data, and assessing recruitment trends by analyzing annual length frequency histograms of the population. In addition to meeting these primary objectives, the study provided other new demographic information, some specific to the Colorado River population (adult survival rate, dispersal patterns, and trends in body condition) and some perhaps applicable to the species in general (growth rate, longevity, and sex ratio).

The 286-km-long study area included the mainstem Colorado River from its confluence with the Green River upstream to the Price Stubb Diversion Dam at Palisade, Colorado and the lower 3.5 km of the Gunnison River downstream of the Redlands Diversion Dam. The 20-km long Westwater Canyon, which separates the 105.7-km upper study reach from the 180.7-km lower reach, was excluded from study; it harbors very few pikeminnow and is difficult to sample. The upper reach, from Westwater Wash to Palisade, was sampled three times annually. The lower reach, from the Green River confluence to Cottonwood Wash, was sampled twice annually. A combination of trammel-netting backwaters and electrofishing shorelines was used to capture as many Colorado pikeminnow as possible during each pass. Fish were measured, weighed, and marked with a uniquely coded passive integrated transponder (PIT) tag inserted in the body cavity. Capture data were used to develop estimates of population abundance, growth rate, dispersal patterns, body condition and length frequency. In 1999 and 2000, captured fish were sexed, and the ratio of males to females in the population was determined. Results of the 1991-1994 sampling have been previously reported; hence, this report emphasizes the results of the 1998-2000 field effort. However, all results are discussed in the context of trends over the past 10 years.

Annual estimates of whole-river population size (all fish $\geq$ 250 mm TL) averaged 582

during the early study period and 742 during the more recent study period, a 27 % increase. Annual estimates of adults (≥ 500 mm TL) averaged 362 during the early study period and 490 during the recent period, representing a 35% increase in adults. Backwater-netting catch rates supported this trend with an increase in rates between 1994 and 1998. However, capture rates declined somewhat after 1998, especially in the lower reach. Interagency standardized monitoring program (ISMP) shoreline-electrofishing results indicated a significant rise in capture rates in both reaches after about 1991. In the upper reach, these rates then remained relatively stable through 2000. However, in the lower reach, ISMP capture rates, after being stable through 1998, declined in 1999 and 2000.

Backwater trammel-netting catch rates of two non-native fish species significantly ($P < 0.05$) increased over the 10-yr period: capture rates of white sucker *Catostomus commersoni* increased from 0.36 to 0.95 fish/net between 1992 and 2000 and black bullhead *Ictalurus melas* capture rates increased from 0.4 to 1.8 fish/net. Additionally, catch rates of the native roundtail chub *Gila robusta* significantly declined from 3.2 to 1.7 fish/net over the same time period.

Dispersal patterns of Colorado pikeminnow were generally similar between periods with a greater percentage of fish in the lower reach moving long distances (> 10 km) between captures (one or more years apart) than fish in the upper reach. In both reaches, the majority of these long-distance movements were in an upstream direction. However, there appeared to be a somewhat smaller percentage of lower-reach fish making long-distance movements during the recent period and a smaller percent moved to the upper reach than during the earlier study period. Also, in contrast to the earlier period, when no fish were found to move from the upper to the lower reach, two fish were detected making such movements during the recent period.

In both 1999 and 2000, males comprised 51% of the population; females, 49%. This result was consistent with the sex ratio of hatchery-reared Colorado pikeminnow reported from Dexter National Fish Hatchery. This 1:1 sex ratio in the wild strongly suggests that mortality is not gender-selective. Length frequency of wild males and females differed, and the greatest number of males occupied the 550-599 mm length-class, whereas the greatest number of females occupied the 650-699 mm length class. Females were also found to attain against point estimates for those years. In most cases there was poor agreement between the predictions and point estimates. Discrepancies suggested that the method, or the abundance point estimates against which the results were compared, is not reliable enough to forecast trends. Imprecision of the point estimates or inaccurate representation of subadults in length frequencies of sampled fish are likely causes for the method failure.

Continuation of the current capture-recapture methodology is recommended for monitoring this population. The three-year-on, three-year-off sampling regimen should also be continued. Back-to-back years of sampling maximize life-history information and allow averaging of annual population estimates; three years of rest allow the population to complete its life functions with minimal disruption. It is strongly recommended that in years of sampling the number of passes and the per-pass effort should be increased to reduce potential bias of abundance estimates and tighten confidence interval width. Concurrent sampling by four crews will be required to accomplish four annual sampling passes in each reach during the eight weeks of spring runoff.

larger size than males: all pikeminnow identified as males in this and other studies have been less than 800 mm long; females from the Colorado River have been as large as 965 mm. New, gender-specific growth curves were constructed based on average annual growth increments. These curves indicated that females grow faster than males, but do not necessarily live any longer. Because all very large pikeminnow were found to be females, the female-specific growth curve was employed to estimate age of the largest fish. Based on these findings, the average age of 900-mm long pikeminnow was revised down to 39 years from an earlier estimate of 56 years.

Average body condition (*Kn*) for almost all length-classes of pikeminnow significantly declined between the early and recent study periods in both reaches. Mean *Kn* of pikeminnow 500-599 mm long was relatively constant in the upper reach during 1998-2000, but significantly increased in the lower reach during the same time period.

As previously reported, length-frequency and scale-aging analyses indicated that many fish recruited from the 1985-1987 year classes, accounting for an increase of adults in the mid-1990s. Especially high spring runoff in 1983-1984 evidently created favorable environmental conditions that resulted in high reproductive success and survival of young during 1985-1987, years of moderately high spring runoff. New data presented here revealed more recent recruitment from the 1990-1994 year classes, although this was lower than for the 1985-1987 year classes. The upper reach length-class containing the greatest percentage of individuals during 1991-1994 was the 550-599-mm-group; however, this shifted to the 600-649-mm-group during 1998-2000. This increase in length of the most common-size fish resulted from the pulse of fish produced during the mid 1980s continuing to grow and work its way up through the age classes.

An experimental exercise in predicting change in adult abundance using population point estimates, growth rates, length frequency, and survival estimates was attempted with mixed results. The estimated number of individuals capable of growing to adult size by the following year was calculated and added to the current-year population point estimate of adults; the number of adults expected to die based on the average annual mortality rate was then subtracted. The resulting predictions of adult numbers in the following year was calculated for all years for which the requisite values were available. These were compared

INTRODUCTION

Colorado pikeminnow *Ptychocheilus lucius* were historically distributed throughout warm-water reaches of the Colorado River basin from Wyoming, Utah, and Colorado south to the Gulf of California (Miller 1961). By the 1970s they were extirpated from the Colorado River basin below Glen Canyon Dam (entire lower basin) and sections of the upper basin as a result of major alterations to the riverine environment (Moyle 1976). Having lost some 80% of its former range, the Colorado pikeminnow was listed as endangered by the U. S. Fish and Wildlife Service (USFWS) in 1967 (Federal Register 32[43]:4001) and was later given protection under the Endangered Species Act (Federal Register39[3]:1175).

Colorado pikeminnow in the upper Colorado River basin presently inhabit warm-water reaches of the Colorado, Green, and San Juan rivers and associated tributaries. The Green River and its two largest tributaries (White and Yampa rivers) support the largest and perhaps most viable (Gilpin 1993) population, while the San Juan River contains the smallest population (Platania et al. 1991). A third population persists in the upper Colorado River, but relatively low catch rates of adults and young during the 1980s (Valdez et al. 1982; Osmundson and Kaeding 1989; McAda et al. 1994) led U. S. Fish and Wildlife Service to conduct an in-depth investigation into the status and trend of this population during 1991-1994. Although Colorado pikeminnow continue to reproduce and new adults are recruited to the population, strong year classes are infrequent and low river-wide abundance of adults limits the long-term viability of the population (Osmundson and Burnham 1998).

After a three-year hiatus following the 1991-1994 sampling, another study was initiated to assess recent population status and assess trends. Annual, systematic, sampling of Colorado pikeminnow ($\geq$ 250 mm long) was conducted throughout their range in the Colorado River mainstem during 1998-2000. The primary goals were to assess population trends by providing new estimates of population size and to assess recent recruitment activity by examining changes in population length frequency. Body condition of fish was also examined as a means to detect trends in food availability. Another goal, not addressed in the earlier study, was to determine the sex ratio of the population. Such information could help refine growth rate and longevity estimates and help refine estimates of the census adult population size needed to provide an effective population size (N_e) of 500, generally believed necessary for maintaining adaptive genetic variation for long-term population viability (Franklin 1980, Allendorf et al. 1997, Rieman and Allendorf 2001).

STUDY AREA

The study area included the portion of the Colorado River upstream of the Green River confluence that is occupied by Colorado pikeminnow (excluding Westwater Canyon), as well as the lower 3.5 km of the Gunnison River from the Colorado River confluence upstream to the base of Redlands Diversion Dam (Fig. 1). Colorado River locations are described in river kilometers (rk) from the Green River confluence and were converted from river miles mapped by Belknap and Belknap (1974) and the Colorado Division of Wildlife (CDOW). In the Colorado River mainstem, the study area extended from the Green River confluence (rk 0.0) upstream to rk 303.0 at Palisade, Colorado, where further upstream movement of fish is blocked by the Price Stubb Dam. For purposes of this study, the study area was partitioned into two major reaches, lower (rk 0-181) and upper (rk 201-303). The upper reach also included the lowermost 3.5 km of the Gunnison River. The lower and upper study reaches are separated by Westwater Canyon. This 20-km canyon reach was not sampled because Colorado pikeminnow are very rare there, with captures averaging only about one per year over a nine-year period, despite intensive sampling associated with other studies (Charles McAda, Recovery Program database manager, personal communication).

METHODS

Capture efforts

A combination of trammel-netting and electrofishing was used to capture Colorado pikeminnow ≥ 250 mm long during late April to mid-June 1998-2000. Trammel nets (1.8 m deep with a 2.5-cm-bar mesh inner panel and a 25-cm-bar-mesh outer wall) were used to

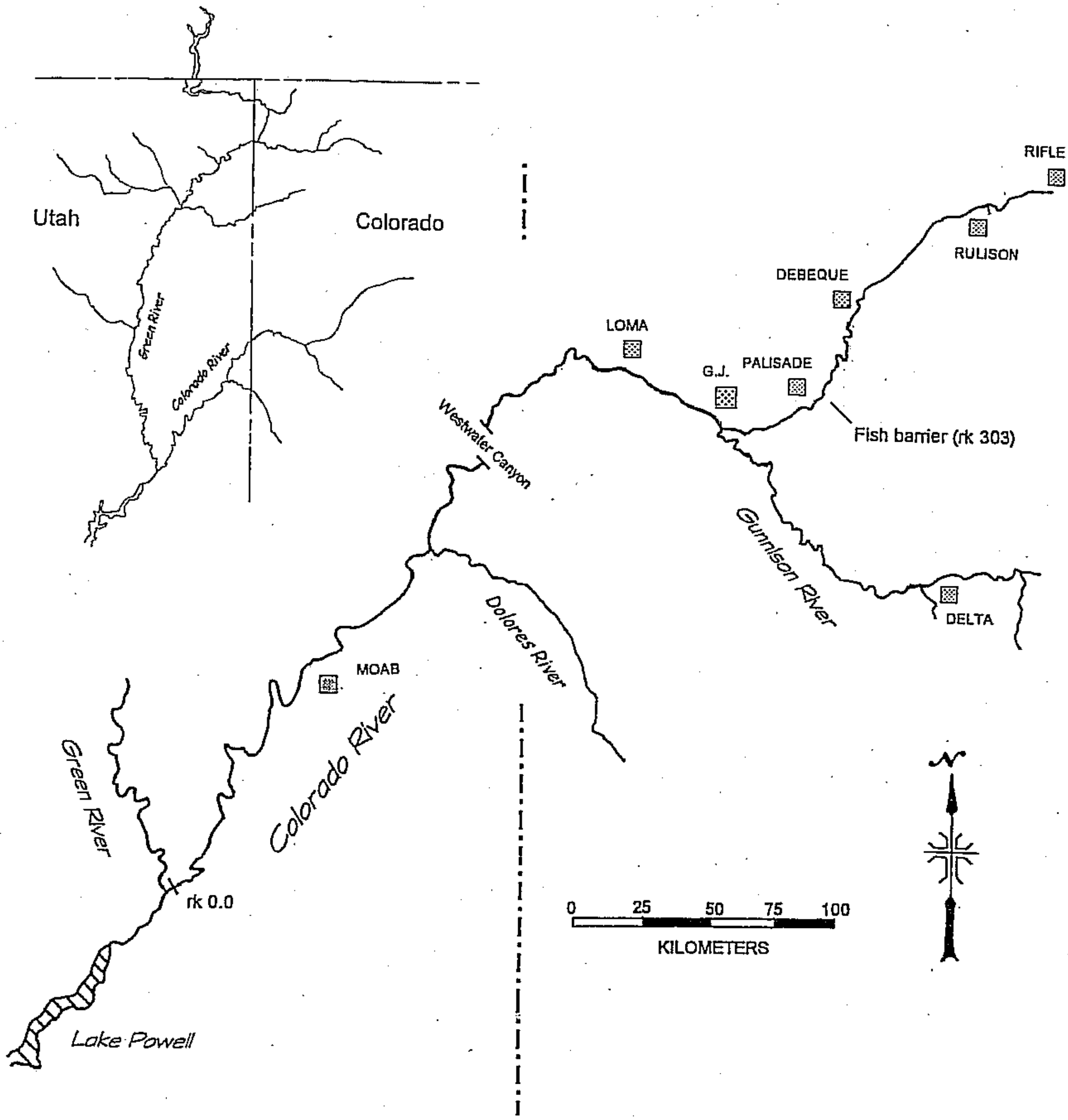

Figure 1. Map of the Colorado river study area. The lower reach extends from the confluence with the Green River (rk 0.0) upstream to the lower end of Westwater Canyon (rk 181). The upper reach extends from the upstream end of Westwater Canyon (rk 201) to the fish barrier at rk 303 and includes the lowermost 3.5 km of the Gunnison River.

capture fish from backwaters throughout the entire study area and electrofishing was used to capture fish from shorelines in reaches where, or at times when, backwaters were few. Subadults and adults congregate in low-velocity, backwater habitats during spring when main-channel flows increase from snowmelt runoff (Osmundson and Kaeding 1989).

Fish were actively entrapped in nets by the 'scare and snare' method (described in Osmundson and Burnham 1998). One net was placed at the mouth of each backwater. For large backwaters, additional nets were set within the backwater once the mouth net was set; the total number set (1-5) increased with backwater size. Ensnared Colorado pikeminnow were placed in a live well until all fish were removed from the nets. Fish were anesthetized with tricane methanesulfonate, measured for maximum total length (TL: Anderson and Gutreuter 1983), weighed with an electronic balance (to the nearest gram) and electronically scanned for the presence of a passive integrated transponder (PIT) tag. If a PIT tag was not found, one was implanted in the body cavity using a hypodermic needle inserted 2-5 mm posterior to the base of the left pelvic fin. Fish were released after recovery from the anesthetic.

Three passes through the upper study reach were made each spring and every backwater deep enough to hold subadult or adult Colorado pikeminnow was netted in each pass. In the lower reach, two passes were made each spring. In each reach, a pass generally took 7-10 days to complete. When electrofishing was employed, both shorelines were electrofished in a downstream direction with a 5-m-long, hard-bottomed, electrofishing boat. In reaches containing rapids, a 5-m-long, rubber raft outfitted for electrofishing was used. Each craft was equipped with a Coffelt VVP-15 that produced pulsed DC. Capture data for portions of some passes were also supplemented with capture records provided by the Colorado Division of Wildlife (lower subreach of the upper study reach), U. S. Fish and Wildlife Service (two flooded ponds in the upper reach) and the Utah Division of Wildlife Resources (most of the lower reach).

Total Abundance Estimation

By grouping sampling periods into sets of three passes within a year, the design corresponded closely enough to the robust design (Pollock 1982) that closed-model capture-recapture methods could be used to estimate population abundance each sample year. This analysis assumes population closure over a time period of about 6-8 weeks. Program CAPTURE (White et al. 1982) was used to estimate abundance from the mark-recapture data (May 16, 1995 version). The simplest model (model M_0 - the null model) of program CAPTURE was used to calculate annual abundance estimates in the upper reach. This model assumes constant within-year capture probabilities (p), but p can vary by year since the annual estimates are done separately. Osmundson and Burnham (1998) chose this model for the upper reach partly because analyses supported constant within-year capture probability, partly due to the sparseness of the data, and because it was supported by the model selection algorithm in CAPTURE. In the lower reach, the use of model M_t to calculate annual abundance estimates was mandated by the sampling regime there that included only two passes. This model assumes capture probabilities vary with time, or in this case, between passes. The estimator Chao M_t assumes not only time variation, but also, unlike Darroch M_t, assumes that there may be some variation in capture probability among fish, even within occasions (passes) and is therefore more robust than Darroch M_t, especially for sparse data and when probabilities of capture are small (Chao 1989, Rexstad and Burnham 1991). Hence, Chao M_t was selected as the lower reach estimator because of the low capture probabilities there and the extreme sparseness of the data.

Adult Abundance Estimation

To estimate size of the adult population, program CAPTURE was run on a subset of the capture records that included only those fish considered adults. However, in one year (1999), when juvenile captures were excluded, there were no recaptures in the lower reach during the second pass, precluding the possibility of a CAPTURE-based estimate for adult abundance there. In this case, a different method for calculating adult abundance was employed. This consisted of multiplying the annual population point estimate for that reach (derived from captures of all fish $\geq$ 250 mm TL) by the proportion of adult-sized fish in the length frequency of all sampled fish $\geq$ 250 mm. For both types of adult abundance estimates, a method for distinguishing adults from juveniles was necessary. The methodology and supporting rationale for this are described in the subsections that follow.

Rationale for using a length-based criterion

Sexual maturity is ultimately what distinguishes an adult from a subadult or juvenile. Although the most definitive measure of sexual maturity is participation in spawning activity, there is no practical means by which to determine whether a captured fish participated in spawning during the previous year or would do so later in the year of capture. Using fish age as a surrogate criterion for distinguishing sexual maturity is also fraught with problems: (1) aging all captured fish (scale analysis) is extremely labor intensive and accuracy cannot be assured, (2) variation in growth among individuals affects age at maturity, making age a poor indicator of sexual maturity, i.e., length interacts with age to determine age at first reproduction (Stearns and Crandall 1984), and (3) length cannot be used to age fish because of the wide overlap in lengths of fish of different ages (see Osmundson et al. 1997). Although there is no doubt variation among individuals and between sexes in size at first reproduction, a minimum length criterion is the most practical approach for categorizing fish as either juveniles or adults.

Rationale for using 500-mm as a minimum-length criterion

For this study, a minimum total length of 500 mm was selected as the criterion for adult status. This was based on length data from fish captured on Colorado River spawning grounds as well as observations of other investigators reporting on maturity of wild fish, as summarized below.

Spawning site surveys have provided some insight into the minimum sizes of Colorado pikeminnow associated with spawning activity. A spawning site electrofished on the Colorado River during 1994, 1998 and 1999 (USFWS unpublished data) yielded 44 individuals (28 running ripe); of these, the smallest ripe male was 489 mm TL and the smallest female was 564 mm TL. Similarly, Tyus (1990) examined 308 Colorado pikeminnow (208 running ripe) trammel-netted from spawning sites in the Green and Yampa rivers during 1981-1988 and reported the smallest ripe male at 435 mm TL and the smallest ripe female at 485 mm TL. It is unknown whether such fish at the low end of the length-frequency range, even though present with larger fish, are indeed viable spawners. Tyus (1990) used 500 mm TL as a minimum length criterion for defining adults. Seethaler (1978) macroscopically examined gonads of 147 preserved specimens and reported 'mature' fish as small as 428 mm TL and immature fish as large as 503 mm TL. Hence, ≥ 500 mm TL is a conservative criterion that results in inclusion of most sexually active fish while excluding many that are not.

Catch Rate

Catch per unit effort (CPUE) of Colorado pikeminnow (mean number of fish caught per net set) was compared among years as an additional means to assess temporal trends in population size. Length of net set varied by backwater width. Length of time the net was set also varied (generally 5-20 min) depending on how many were set or how long it took to remove fish from other nets. Hence, capture effort associated with a 'net set' could not be standardized in the conventional sense to allow comparisons of netting capture rate among sites. However, with a relatively large sample of net sets, the average effort per net set can be assumed to be essentially equal among years, given that the same backwaters are sampled each year and the same protocols followed. This allows among-year comparisons of average netting capture rates within reaches. It is also important to note that the 'scare-and-snare' technique is an active netting method rather than a passive one. This is important because the length of net in the water and the period the net is allowed to fish becomes less relevant if most or all of the fish in a backwater are scared or 'driven' into a net.

In addition to the trammel-netting CPUE described above, shoreline electrofishing capture rates from the adult portion of the Interagency Standardized Monitoring Program (ISMP) for the 1992-2000 period were used as a consistency check for discerning trends in population abundance (for methods, see McAda et al. 1994).

Annual catch rates of sympatric species in the upper reach were also examined for trends in abundance. Seven species (three native; four nonnative) comprise most of the large-bodied fish community. Changes in abundance of these sympatric species affect community structure, potentially affecting levels of food availability for Colorado pikeminnow and perhaps levels of predation, competition, and in the case of spined species, choking mortality (see McAda 1983, Ryden and Smith 2002). Again, mean number of fish captured per net set was the index of relative abundance.

Dispersal

Movements of Colorado pikeminnow during 1996-2000 were summarized and compared with movements during 1991-1995. Capture records from the intensive 1998-2000 study were supplemented with records from 1996 and 1997, obtained from annual ISMP spring electrofishing surveys (McAda 2002) as well as other studies. These other studies included surveys of ponds at rk 263-265 (Scheer 1998) and in the 15-mile reach at rk 281 (Burdick et al. 1997), and from electrofishing surveys of the lower Gunnison River and daily trap records from the Redlands fish ladder (Burdick 2001). Only movements between consecutive captures at least one year apart were considered. Long-distance movements were considered those greater than 10 km (6.2 mi); those less than 10 km were considered localized movements and disregarded. Criteria and methods follow those previously described by Osmundson et al. (1998).

Sex Ratio

Gender of captured Colorado pikeminnow was determined by visually examining the urogenital area anterior to the vent. Colorado pikeminnow are not noticeably sexually dimorphic and difference in genitalia morphology appears to be the only external characteristic that can be used to distinguish the sexes when milt or eggs cannot be expressed. Males possess a genital papilla whereas females have a fleshy genital sinus. However, the difference in the structure of these organs is not readily apparent to the untrained observer, particularly in young specimens. I learned to distinguish these differences at Dexter National Fish Hatchery (NFH) in March of 1999, prior to the beginning of the second year of sampling. A description of this preliminary training is outlined below so as to allow the reader to better judge the validity of the method.

At Dexter NFH, fish culturist Roger Hamman instructed me in identifying the characteristics that distinguish male from female Colorado pikeminnow. A blind test was then conducted by both of us on a sample of 107 1991 F_1 Colorado pikeminnow (426-593 mm TL) and the gender of each fish was recorded independently. Results indicated 100% concurrence between us in gender identification. This exercise was then followed by my examining another 60 individuals. As before, the sex of each was recorded based on an examination of the external characteristics of the genitalia; however, this time each fish was then sacrificed and the true gender was verified by the presence of either testes or ovaries. Misidentification of gender occurred twice resulting in a 97% success rate.

In the field, determinations of gender of captured fish were made by me. Those records with gender noted by other investigators when I was not present were not used in the sex-ratio analysis.

Growth Rate

All fish

Growth rate of Colorado pikeminnow was previously estimated for the earlier 1991-1994 study using a combination of scale ageing of measured individuals and calculating average growth increments of recaptured fish of various size classes (Osmundson et al. 1997). In the more recent field effort, no scale ageing was done, but additional data on growth of recaptured fish were used to increase sample sizes and refine earlier estimates of average annual growth increments. This was first done for the population as a whole and then done on a gender-specific basis (see below).

Analyses indicated that one source of error in annual growth increment measurements is that caused by using data collected by different investigators, i.e., an individual fish captured on one date by one investigator and then recaptured and measured by a different investigator. Because growth increments are generally small, small differences in measuring technique can over- or under-estimate annual growth increments. For instance, I prefer to anesthetize Colorado pikeminnow before measuring them whereas many other investigators do not do so. When anesthetized, fish are relaxed and lie flatter on the measuring board compared to non-anesthetized fish. This often results in measurements 5-10 mm more than if fish are not anaesthetized. With additional measurements from the recent study, a larger total sample size allowed greater discrimination in the selection of data used in recalculating average growth increments. For the new analysis, the goal was to use only measurements from fish captured and recaptured by me in an attempt to minimize this source of error.

Although adding the new data initially doubled sample size, imposing the more stringent criteria greatly reduced usable values; this resulted in a final sample size similar to that used in the prior analysis by Osmundson et al. (1997). These criteria had to be relaxed to obtain a sample for the 800-850- and 900-949-mm-TL length-classes. For these length-classes, measurements taken by other investigators were also used. Also, for all length-classes greater than 700 mm, averaged increments were used to bolster sample sizes (averaged increments are those derived by taking the difference in length of a fish captured more than one year apart (2-8 yr) and dividing the increment by the number of years between captures). For length-classes less than 700 mm only increments from fish captured one year apart were used.

Gender-specific

Difference in growth rate between males and females was also quantified in an effort to further refine the calculation of average age at various lengths. The gender identifications from 1999 and 2000 provided a unique opportunity to calculate growth rates separately for males and females. To do this, the 1990-1999 database (years for which pit tags were used to mark fish) was searched for all previous captures of each fish for which there was now a gender identification. As before, growth increments were calculated by examining differences in total length between captures. Each increment was assigned to the 50-mm length class that corresponded to the length of the fish at the first of two consecutive captures. To increase sample size, data were used not only from captures one year apart but also from captures separated by two or more years; these increments were divided by the number of years separating captures (see previous section). Multiple-year increments were not used if a fish occupied more than two 50-mm length-classes between captures (for example: an increment would not be used from a fish measuring 475 mm at first capture and 575 mm at second capture, having been in three separate length-classes during the intervening period). Without these restrictions, the calculated average annual increment may not represent the increment for the length-class at first capture. Length increments were used from captures by all investigators provided that the same individual or crew made both the initial and subsequent measurements. For females, gender identification was available for fish captured in 1999 and 2000 only; for males, samples were supplemented with fish captured in previous years when sex was positively known from field notes indicating a running ripe condition.

Body Condition

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

$$Kn = \frac{M_o}{M_e} * 100$$

The expected mass (M_e) is calculated using constants derived from mass-length regressions:

$$Log_{10}Me = ((Log_{10}\text{ length})\text{ slope}) + \text{y-intercept}$$

The constants for these month-specific mass-length regressions were previously derived from Colorado pikeminnow captured from the Colorado River during 1991-1994 and provided in Osmundson et al. (1998). Relative condition of each fish was calculated using the constants specific to the month during which the fish was captured. Mean Kn was then compared between upper and lower reaches within 100-mm length-classes and among length-classes within reaches.

Length-frequency

To detect recent changes in population size structure, 50-mm length-frequency histograms were developed so that comparisons could be made between recent years and the 1991-1994 period. Separate annual histograms were produced for the lower and upper reach, and pooled multi-year histograms were produced for the upper reach to allow comparisons between periods.

Predicting Change in Adult Numbers

Length-frequency and growth-rate information can be utilized to estimate expected recruitment for the following year. Population estimates and adult survival rate information can be used to estimate the number of adult fish expected to die in the following year. Together, these results can provide a prediction of change in adult numbers from one year to the next. Over a series of years, these annual predictions can provide insight into the ability of the population to replace itself. Secondly, they provide a consistency check for similar estimates of change based solely on differences in annual population point estimates. This exercise was attempted using data from the two intensive sampling periods of the 1990s; the methods and rationale are outlined below.

To recruit to adulthood (defined here as attaining 500 mm TL) fish must be able to grow from their length in the present year (denoted as year *i*) to at least 500 mm by the following year (year $i + 1$). The growth rate information allows calculation of a mean growth increment for fish 450-499 mm long. Subtracting this increment from 500 gives the minimum length a fish must be at year *i* to attain 500 mm by year $i + 1$. Some fish, such as females, will grow faster and thus can start smaller; others will grow slower and therefore must initially be larger; however, for this exercise, use of the mean value should account for this.

The length-frequency data provides an estimate of the percent of the population in year *i* that consists of individuals about to recruit (those with lengths between the minimum calculated size and 500 mm TL). This proportion can be applied to the population point estimate to arrive at an estimate of the actual number of fish in this category. Because the upper and lower reach was sampled with unequal effort, length frequency data were not combined. Instead, the number of fish about to recruit was calculated separately for each reach and then values were summed to provide a whole-river estimate.

Next, the number of adults that die each year was accounted for by using population mortality estimates developed in previous studies. Osmundson et al. (1997) and Osmundson and Burnham (1998) provided adult annual survival rate estimates for Colorado pikeminnow of 85% (for fish > 550 mm) and 86% (upper-reach fish), respectively. For this exercise, survival rate was assumed to be fairly constant and the 86% survival value (14% annual mortality) was applied to the whole-river adult population estimate for year i to arrive at the number of adults surviving to year $i + 1$. These estimates of recruitment and mortality were then used to estimate the expected number of adults in year $i + 1$. The net gain or loss is expressed in either numbers or percent of the population at year i.

Statistical Analyses

Different statistical procedures were performed to make between-reach or among-year comparisons of various biological metrics (population estimates, capture rates, mean body condition, etc.). A z-test was used to compare the averaged 1992-1994 whole-river population estimate with that of the 1998-2000 whole-river estimate. Analysis of variance (ANOVA) was used to test for among-year differences in catch rates (pikeminnow and sympatric species netting, pikeminnow ISMP electrofishing); when significance ($P < 0.05$) was indicated, Fisher's LSD Multiple-Comparison Test was used to determine which years were significantly different from one another. A two-sample t-test was used to test for differences in Colorado pikeminnow growth increments derived from 1991-1994 data and those derived from 1991-2000 data; it was also used to test for differences between male and female growth increments within various length-classes. ANOVA and Fisher's LSD Multiple-Comparison Test was used to test for differences in Colorado pikeminnow body condition among years, between study periods, and between sexes. All statistical analyses were performed using NCSS (2000).

RESULTS AND DISCUSSION

Estimates of Total Population Size

Annual estimates of population size were calculated separately for the lower and upper reaches because the numbers of sampling passes in the two reaches were unequal (three passes in the upper; two in the lower). However, the separate estimates were summed to provide annual estimates of whole-river population size, and these in turn were averaged to provide one estimate to describe general population size for each study period (Tables 1 and 2).

For the upper reach, the population size point estimate (95% C. I. in parentheses) was 441 (322-642) for 1998; 356 (273-494) for 1999; 463 (300-775) for 2000. For the lower reach, point estimates were 282 (171-544), 324 (144-893) and 359 (134-1,213) for 1998, 1999 and 2000, respectively. Summing the point estimates resulted in whole-river estimates of 723 (489-957) for 1998, 680 (331-1029) for 1999 and 822 (309-1335) for 2000. The 3-yr average estimate for the whole river was 742 individuals (521-963). These numbers include both adult ($\geq$ 500 mm long) as well as juvenile fish from 250 to 499 mm long. This represents an estimated increase of 160 fish from the earlier 1991-1994 period; the whole-river, 3-yr average (1992-1994) at that time (no lower reach estimate in 1991) was 582 (385-779) fish (Table 2). Results of a Z-test used to compare estimates indicated that population size was not significantly different ($Z = 0.247$; $P = 0.805$) between the early and recent periods. Comparing annual estimates, wide confidence intervals precluded significant differences among years with the possible exception of the upper-reach estimate for 1993 which appears to be significantly lower than the estimates for the three recent years, 1998, 1999 and 2000 (Fig. 2).

One measure of estimate precision is the coefficient of variation (CV: $SE/\hat{N} \times 100$). Pollock et al. (1990) suggests a good 'rule of thumb' is to achieve a CV of 20% or less (see Appendix Table III for CV's attained in this study). For all Colorado pikeminnow, a CV $\leq$ 20% was achieved in the upper reach in 1993, 1998 and 1999. This level of precision was

Table 2. Annual population size estimates for the entire Colorado River study area. Lower and upper reach estimates were summed for each year (from Table 1) to provide annual whole-river estimates. The annual whole-river estimates were then averaged over two 3-yr periods, 1992-1994 and 1998-2000 (in bold). Because there was no lower-reach estimate for 1991, no whole-river estimate is provided for that year. Similarly, Program CAPTURE could not calculate an estimate for fish ≥ 450 mm or for fish ≥ 500 mm in the lower reach in 1999 because there were no recaptures of fish in these size ranges; hence, estimates were derived by multiplying the population point estimate for all fish ≥ 250 mm by the percent of the population consisting of individuals ≥ 450 and ≥ 500 mm, respectively. These estimates were added to the upper-reach mark-recapture estimates and the sums are provided (marked with an asterisk*). For these, no whole-river confidence intervals could be calculated.

	Whole River					
Year	Pop est fish≥250 mm	95% CI	Pop est fish≥450 mm	95% CI	Pop est fish ≥500 mm	95% CI
1991	no est	--	no est	--	no est	--
1992	532	145-919	382	75-702	324	65-603
1993	598	252-944	476	222-730	255	126-384
1994	617	335-897	652	237-1067	507	205-809
92-94	**582**	385-779	**503**	309-697	**362**	218-506
1998	723	489-957	583	365-801	507	313-701
1999	680	331-1029	512*	--	398*	--
2000	822	309-1335	719	318-1120	564	292-836
98-00	**742**	521-963	**604**	--	**490**	--

Table 1. Annual population size estimates for the lower and upper reaches of the Colorado River study area for the 1991-1994 and 1998-2000 periods. Annual point estimates and 95% confidence intervals are from program CAPTURE (May 16, 1995 version); upper reach: Model M_0; lower reach: Model M_t (Chao 1989). Program CAPTURE could not provide an estimate for fish $\geq$ 450 mm or for fish $\geq$ 500 mm in the lower reach in 1999 because there were no recaptures of fish in these size ranges; hence, estimates (no confidence interval possible) provided were derived by multiplying the population point estimate for all fish $\geq$ 250 mm by the percent of the population (from length frequencies of captured fish) consisting of individuals $\geq$ 450 and $\geq$ 500 mm, respectively.

	Upper Reach						Lower reach					
Year	Pop est fish≥250 mm	95% CI	Pop est fish≥450 mm	95% CI	Pop est fish ≥500 mm	95% CI	Pop est. fish ≥250 mm	95% CI	Pop est fish ≥450 mm	95% CI	Pop est fish ≥500 mm	95% CI
1991	215	123-442	202	116-413	197	107-433	--	--	--	--	--	--
1992	381	181-927	358	171-872	316	153-767	151	63-503	24	15-74	8	7-22
1993	163	123-242	153	115-226	130	96-200	435	226-967	323	172-712	125	63-336
1994	368	225-667	368	225-667	337	193-661	249	137-543	284	111-954	170	72-562
1998	441	322-642	420	307-611	394	290-573	282	171-544	163	79-443	113	49-374
1999	356	273-494	339	261-470	307	236-427	324	144-893	173	--	91	--
2000	463	300-775	456	296-763	415	271-692	359	134-1213	263	103-883	149	63-495

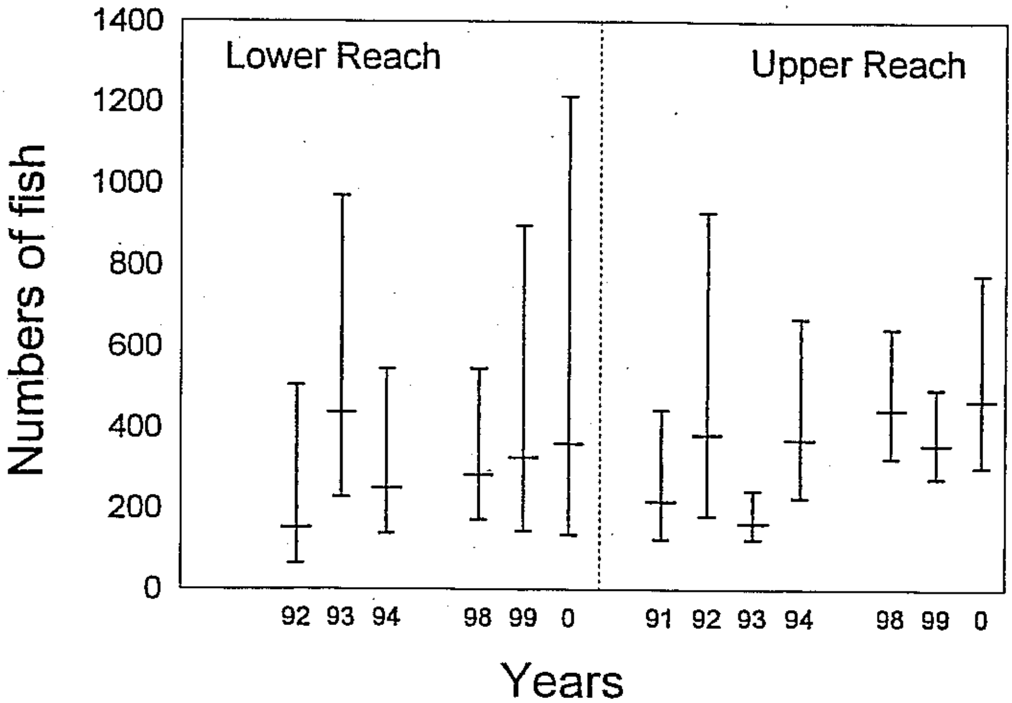

Figure 2. Annual population estimates of Colorado pikeminnow ($\geq$ 250 mm long) for the lower reach (model M_t) and upper reach (model M_0). Error bars represent 95% confidence intervals.

never met in the lower reach. For the combined lower- and upper-reach estimates, only 1998 had a CV $\leq$ 20 % ($\hat{N}$ = 723, SE = 119.52, CV = 16.5).

Estimates of Adult Population Size

In the upper reach during 1998-2000, the percent of captured fish that were 500 mm long or longer ranged from 90 to 95%, depending on the year. This was similar to 1991 (90%) and 1992 (95%), but higher than in 1993 (81%) and 1994 (83%). Hence, the number of adults in the upper-reach was not much less than that of the total number of pikeminnow ($\geq$ 250 mm TL) there. Annual estimates of adults were 394 in 1998, 307 in 1999, and 415 in 2000 (Table 1). The average for the 3-yr period was 372 adults.

In the lower reach, the percent of the population consisting of adults was substantially less than that in the upper reach (Fig. 3). Also, variation in this percentage was much higher

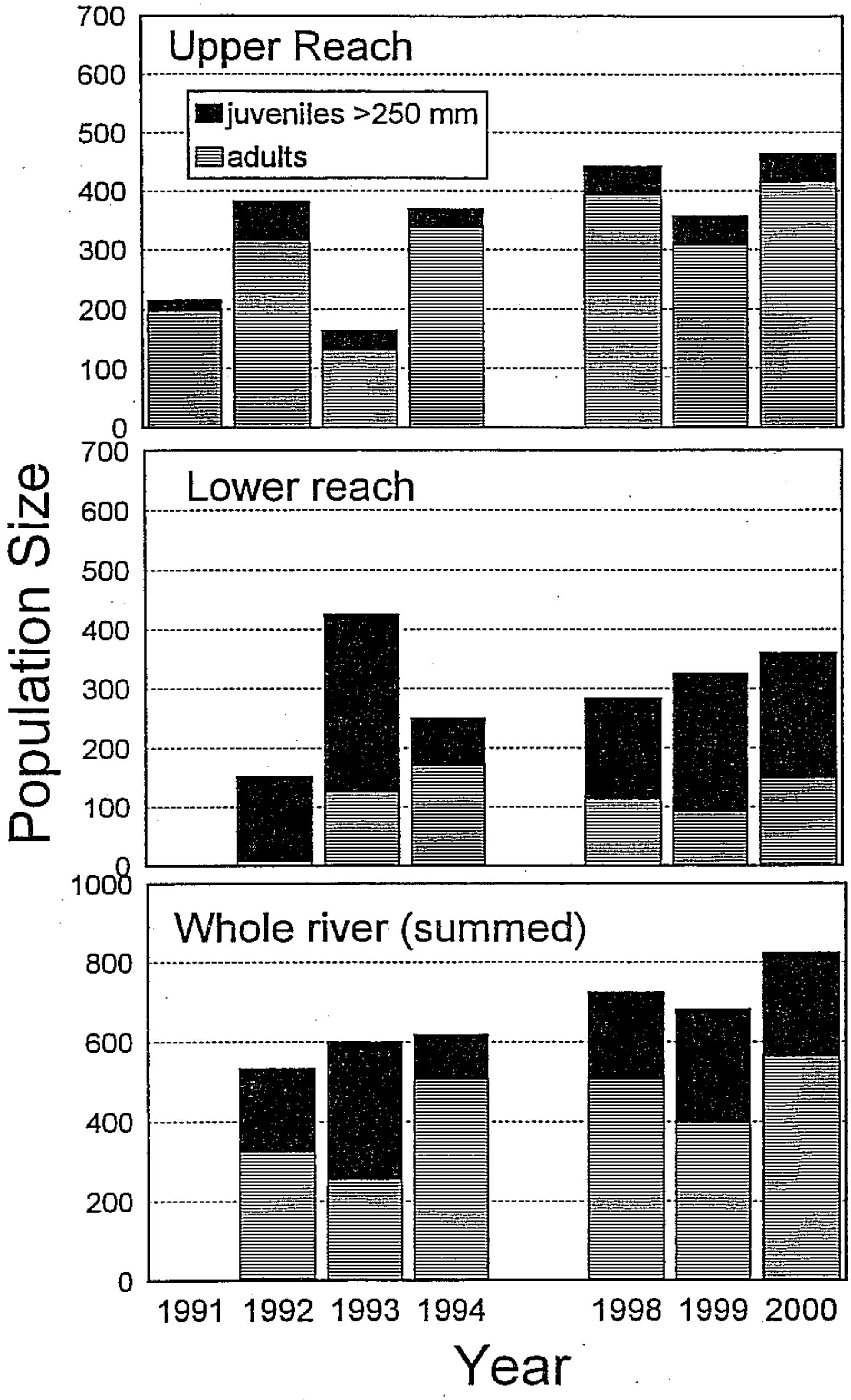

Figure 3. Numbers of adults (≥ 500 mm TL) in relation to the total sampled population (≥ 250 mm TL) in the upper reach (top), lower reach (middle) and the whole river (bottom).

among years (33-64% during 1998-2000) than in the upper reach. This was also the case during the earlier 1991-1994 study period when adults made up from 3% (1991) to 56% (1994) of lower-reach captures. Annual abundance estimates for the lower reach during 1998, 1999 and 2000 were 113, 91 and 149 adults, respectively. The 3-yr average was 118 adults.

The estimated number of adults in the whole study area appears to have increased from the 1992-1994 period to the more recent 1998-2000 period. Averaging the annual summed estimates provided a whole-river estimate of 490 adults for the recent period compared to 362 adults estimated for the earlier 1992-1994 period. These averaged point estimates suggest a 35% increase in adults from the 1992-1994 to 1998-2000 periods.

A draft document that establishes goals for recovery of Colorado pikeminnow (see U. S. Fish and Wildlife Service 2002a) uses ≥ 450 mm as a length criterion for defining adult status. Because population targets for recovery are specified in number of adults rather than total fish, the number of Colorado pikeminnow ≥ 450 mm long were also calculated and are provided here in Tables 1 and 2.

For Colorado pikeminnow ≥ 500 mm long or 450 mm long, the 'rule of thumb' for acceptable estimate precision (CV of ≤ 20%) was met only in the upper reach in 1993, 1998 and 1999 and was never met in the lower reach. For whole-river estimates, adequate precision for fish ≥ 500 mm long was obtained in 1998 ($\hat{N}$ = 507, SE = 98.98, CV = 19.5) and 1999 ($\hat{N}$ = 376, SE = 76.91, CV = 20.4). For Colorado pikeminnow ≥ 450 mm long, adequate precision was met only in 1998 ($\hat{N}$ = 583, SE = 111.06, CV = 19.0).

Catch Rates

Mean CPUE (captures per net set) of Colorado pikeminnow (≥ 250 mm TL) in the upper reach increased between the early and more recent periods (Fig. 4). Differences among years were statistically significant (ANOVA; $P = 0.000016$); CPUE was significantly higher ($P < 0.05$) in 1998 than in 1991, 1992, 1993 and 1994; CPUE in 1999 and 2000 were each significantly higher than in 1991 and 1992. This was consistent with results from the mark-recapture population point estimates that also indicated a population increase during the 9-10

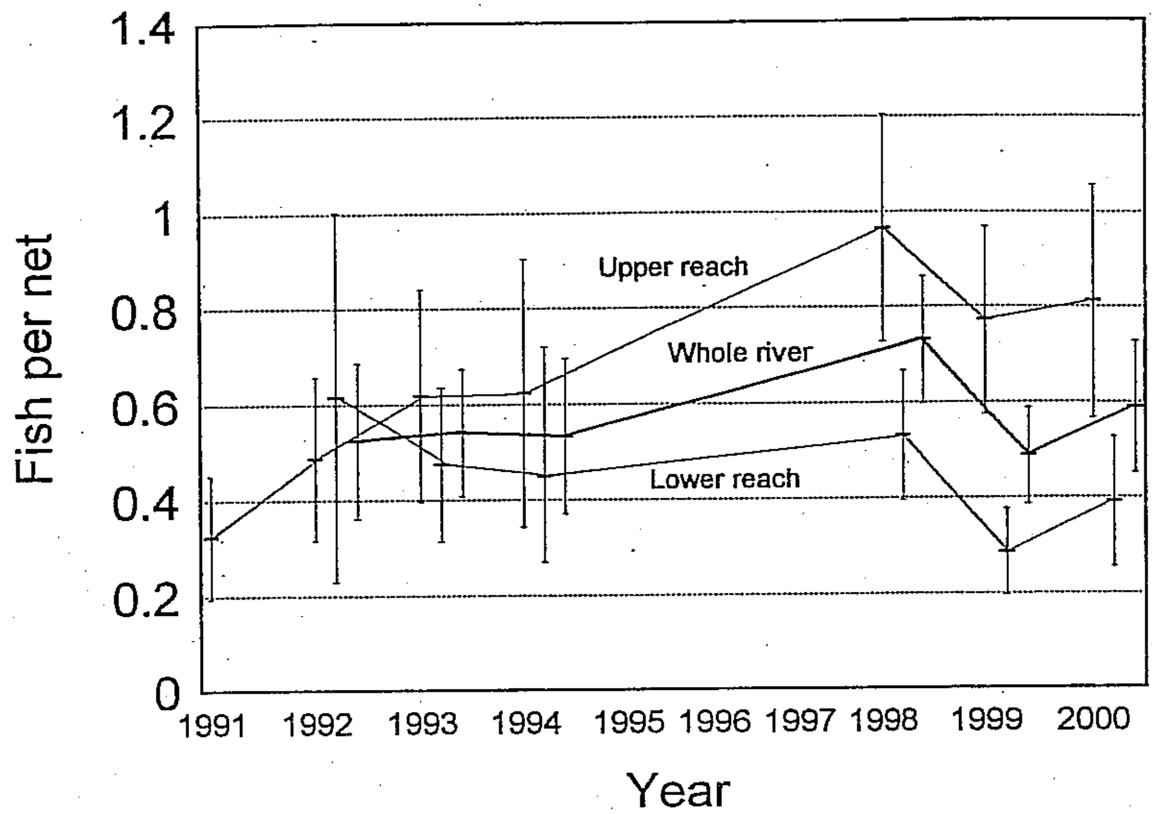

Figure 4. Catch rates (fish/net) of Colorado pikeminnow in backwaters of the upper reach, lower reach and the whole river. Error bars represent 95% confidence intervals.

year period. Capture rates of the three recent years (1998-2000) were not significantly different ($P > 0.05$) from one another, although 1998 had the highest absolute value, suggesting the population may have reached a peak during this or one of the three previous years (1995-1997) not sampled.

In the lower reach, mean number of fish per net appeared to decline between 1992 and 1994 and may have increased a little by 1998; however, by 1999 and 2000, mean catch rates had dropped to the lowest values recorded for the seven years of sampling (Fig. 4). Because of high variation among net sets, no differences among years were statistically significant (ANOVA; $P = 0.165$).

As lower-reach capture rates appeared to decline between 1992 and 1994, upper-reach capture rates increased, a result consistent with dispersal data demonstrating that many recent recruits in the lower reach were migrating to the upper reach during this period (see

Osmundson et al. 1998). Whole-river capture rates (calculated by combining annual upper- and lower-reach data sets) were virtually unchanged through these years (Fig. 4). However, during 1998-2000, annual whole-river capture rates tracked upper- and lower-reach trends: rates at first appeared to increase, then decreased and then increased again. There appeared to be much more variability among years during the late 1990s than during the early 1990s. Differences among all seven years were statistically significant (ANOVA; $P = 0.044$); mean catch rate in 1998 was significantly higher ($P < 0.05$) than in 1992, 1993, 1994 and 1999; it was not significantly higher than in 2000.

Catch-rate results from ISMP (captures per hour of shoreline electrofishing) serve as an important consistency check on population estimates and backwater-netting catch rates when inferring trends in abundance. Like the population estimation sampling regime, ISMP divides the Colorado River into upper and lower reaches separated by Westwater Canyon. However, the upper-reach study area, includes only the Loma-to-stateline subreach and excludes the Grand Valley. In the lower reach, catch rates are derived by pooling results of two sampling sub-reaches (McAda et al. 1994, McAda 2001).

Total numbers of Colorado pikeminnow captured in the ISMP upstream sampling area have been comparatively low (0-11 fish per year), resulting in high catch-rate variability within years. Nevertheless, mean catch rates were consistently higher after 1990: annual means averaged 0.25 fish/hr during 1986-1990 and averaged 1.30 fish/hr during 1991-2000 (Fig. 5), and differences among years were statistically significant (ANOVA; $P = 0.024$). However, only 1991, 1995 and 1999 had significantly higher ($P < 0.05$) catch rates than other years; these years were higher than 1986, 1987, 1988, 1989, 1990 and 1992. After 1991, there was no trend of catch rates continuing to increase (McAda 2001).

In the lower reach, annual ISMP catch rates were consistently low from 1986 to 1991, averaging 0.6 fish/hr (Fig. 5). From 1992 to 1998, annual catch rates were consistently higher, averaging 1.7 fish/hr. Differences among years were statistically significant (ANOVA; $P = 0.000000$). With the exception of 1993, mean catch rates during 1992-1998 were significantly higher ($P < 0.05$) than in all six previous years. Mean catch rate in 1993 was significantly lower ($P < 0.05$) than in 1992, 1996, 1997, and 1998. The six years of 1992, 1994, 1995, 1996, 1997 and 1998 were not significantly different from one another and no

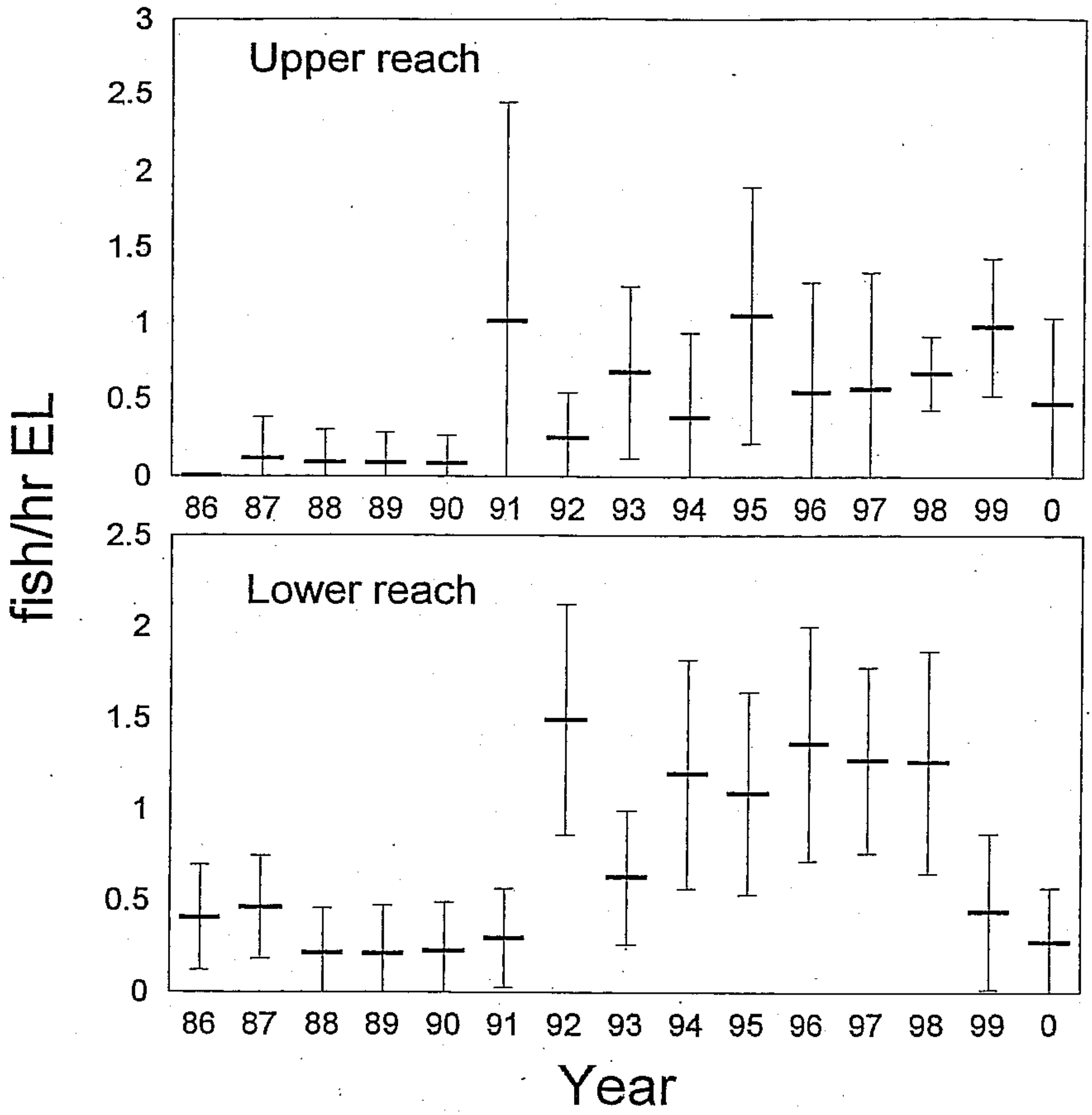

Figure 5. ISMP catch rates (fish/hr of electrofishing) of Colorado pikeminnow along shorelines in sub-reaches of the upper and lower reaches. Error bars represent 95% confidence intervals. Interagency Standardized Monitoring Program data summarized and provided by Charles McAda (USFWS).

trend of increasing numbers was indicated. In 1999 and 2000, catch rates were once again low, averaging 0.7 fish/hr; the mean catch rate in both years was significantly lower ($P < 0.05$) than the five annual means from 1994 to 1998.

Catch Rates of Sympatric Species

Fish occasionally produce strong year classes resulting in increased catch rates as these cohorts grow and become susceptible to capture. If recruitment rate is less than mortality rate, densities (and catch rates) decline. Thus, annual variation in CPUE is expected. Physical or biotic environmental change may produce conditions that affect recruitment or survival rates of some species. If an imbalance between recruitment and survival rates persists, long-term trends in population size may become evident. These changes in community structure, either short-term or long-term, are of interest because they affect the biotic environment in which Colorado pikeminnow live. Our netting results provide some insight into the population dynamics of members of the Colorado River fish community over a ten-year period.

As described earlier, Colorado pikeminnow in the upper reach displayed a general increase in netting catch rate over the 10-year period. Catch rates of another native fish, roundtail chub *Gila robusta*, declined over the same period (Figs. 6 and 7). Mean CPUE was significantly different among years (ANOVA; $P = 0.0047$), with means in 1998 and 1999 significantly lower than in 1992, and the mean in 2000 significantly lower than in 1992, 1993 and 1994. Catch rates of the native bluehead sucker *Catostomus discobolus* were also significantly different among years (ANOVA; $P = 0.000000$); however, like Colorado pikeminnow, an increase through 1998 was followed by declines in 1999 and 2000. Catch rates in 1998 were significantly higher ($P < 0.05$) than in 1992, 1993, and 1994, whereas catch rates in 1999 and 2000 were significantly lower than in 1998 (Fig. 7). Bluehead suckers are not attracted to backwaters during spring runoff like some other main-channel species and their comparatively low catch rates reflect this (Fig. 6). Although catch rates in backwaters provide an index to changes in bluehead sucker population abundance, trends for this species would be better assessed with main-channel sampling. Flannelmouth suckers *Catostomus*

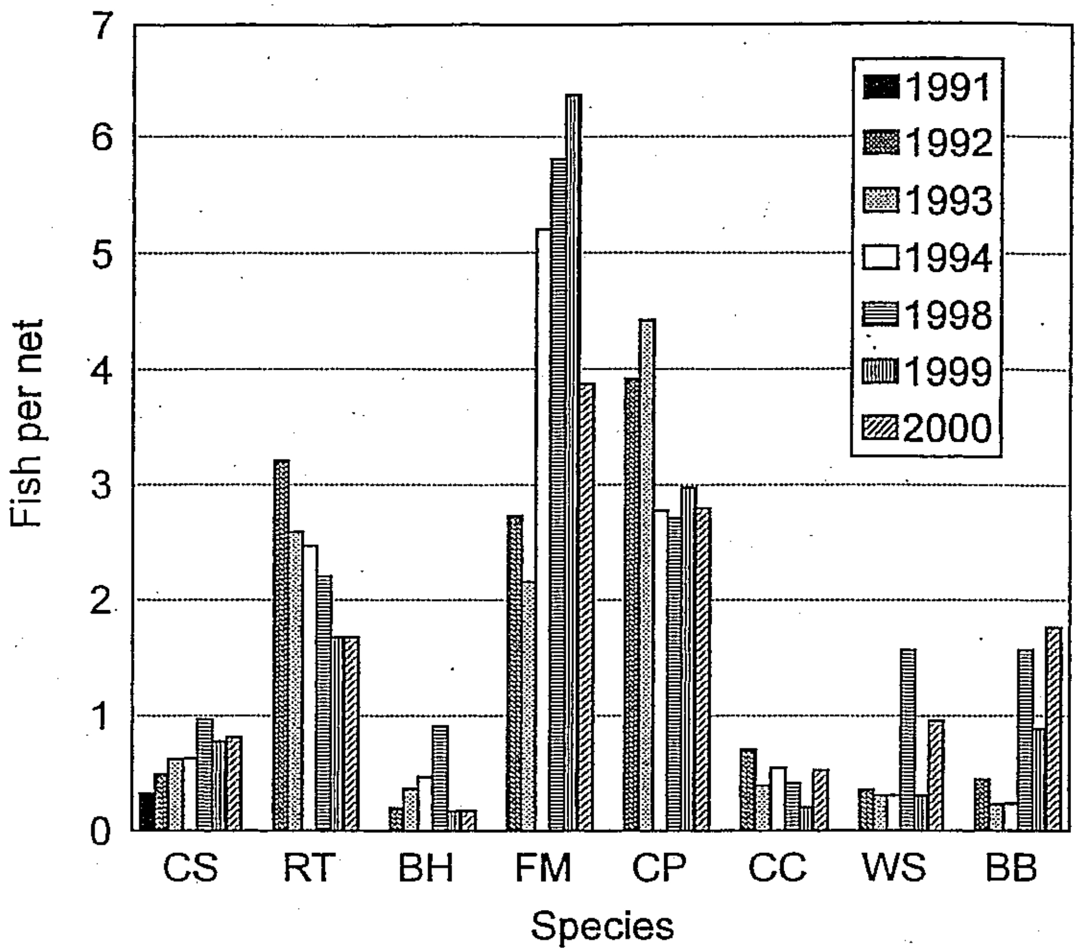

Figure 6. Annual mean catch rates (fish/net) of eight large-bodied fish species in backwaters of the upper reach. CS: Colorado pikeminnow; RT: roundtail chub; BH: bluehead sucker; FM: flannelmouth sucker; CP: common carp; CC: channel catfish; WS: white sucker; BB: black bullhead.

latipinnis, on the other hand, use backwaters extensively during spring and their catch rate also significantly differed among years (ANOVA; $P = 0.0019$). Catch rates in 1994, 1998 and 1999 were significantly higher ($P < 0.05$) than in 1992 and 1993. Mean catch rate in 2000 declined somewhat (Fig. 7), and was significantly lower than in 1994 and 1998. For both bluehead and flannelmouth sucker, no consistent trend was apparent over the 10-year period.

Trends in catch rates of non-native fish varied by species. Common carp *Cyprinus carpio* was the most abundant nonnative species captured from backwaters and catch rates appeared to decline after 1993 (Fig. 8), but differences among years were not statistically significant (ANOVA; $P = 0.327$). For channel catfish *Ictaluras punctatus*, differences among

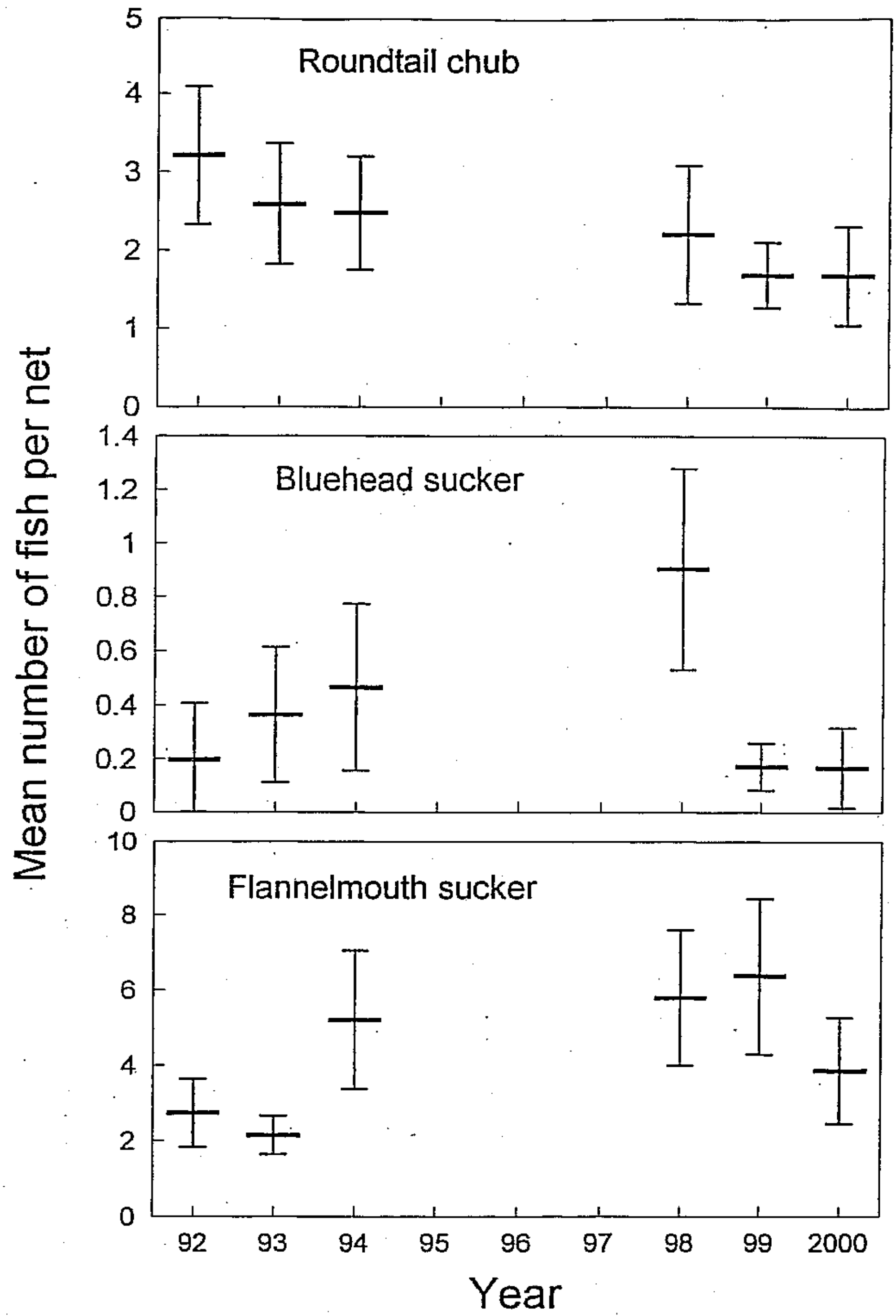

Figure 7. Annual catch rates (fish/net) of three sympatric large-bodied native fish species in backwaters of the upper study reach. Error bars represent 95% confidence intervals.

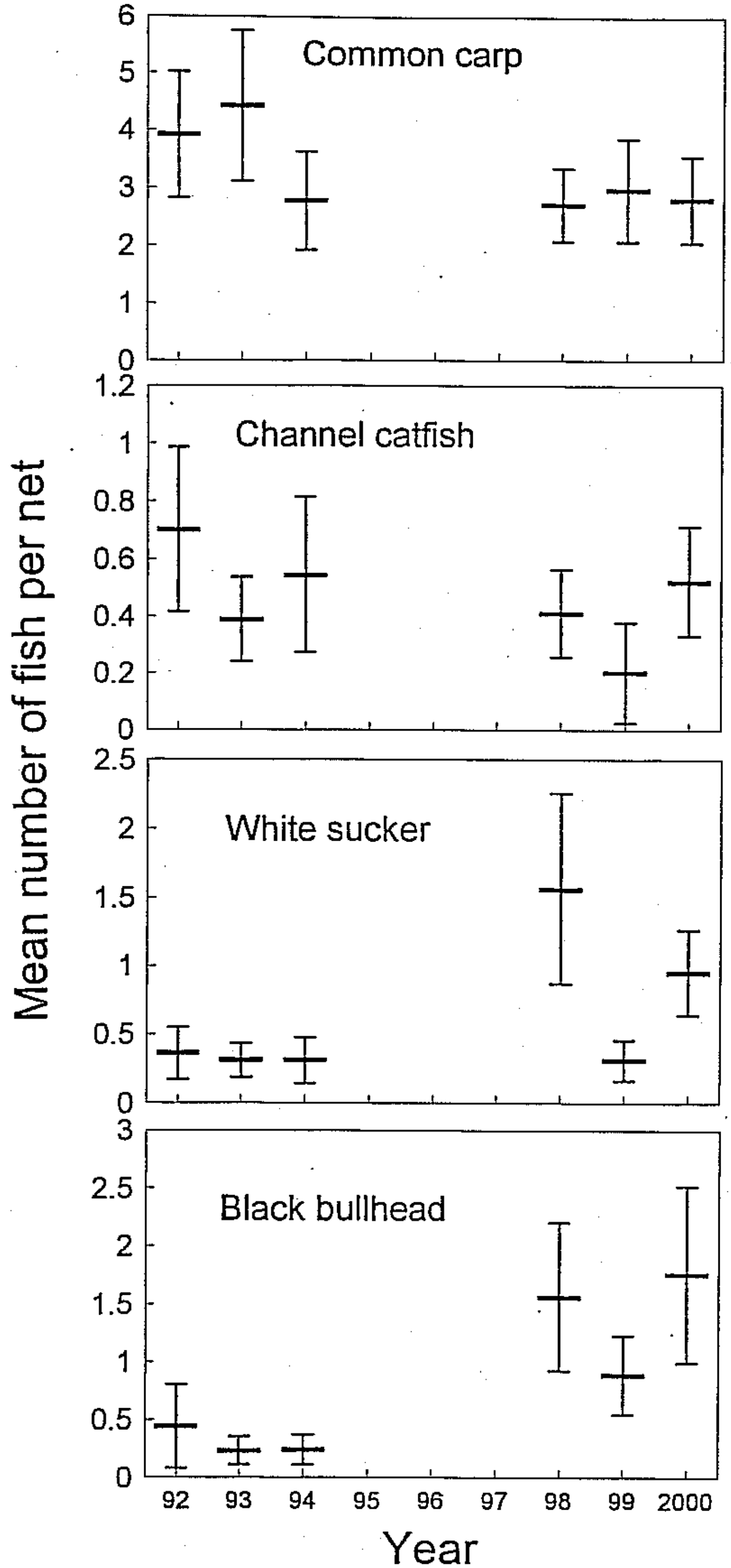

Figure 8. Annual catch rates (fish/net) of four sympatric large-bodied non-native fish species in backwaters of the upper study reach.

years were statistically significant (ANOVA; $P = 0.0025$), but only the 1999 catch rate differed from other years, and it was significantly lower ($P < 0.05$) than all five other years; hence, no consistent trend was evident (Fig. 8). White sucker *Catostomus commersoni*, an introduced catostomid that hybridizes with native sucker species (Burdick 1995), evidently increased in abundance from the early to the late 1990s (Fig. 8). Differences among years were statistically significant (ANOVA; $P = 0.000000$). Although mean catch rate was low in 1999, rates in 1998 and 2000 were significantly higher ($P < 0.05$) than in 1992, 1993 and 1994. Catch rates of black bullhead *Ictalurus melas* also indicated an increase in abundance (Fig. 8). Differences among years were statistically significant (ANOVA; $P = 0.000000$); mean catch rates in 1998, 1999 and 2000 were significantly higher ($P < 0.05$) than in 1992, 1993 and 1994.

Dispersal

During the 1998-2000 study period, 156 different Colorado pikeminnow were recaptured at least once. The first capture of 34 of these fish during this period occurred in the lower reach; the first capture of the other 122 fish occurred in the upper reach. Some of these individuals were recaptured two or more times: for fish first captured in the lower reach, there was a total of 37 recaptures; for fish first captured in the upper reach, there were 160 recaptures.

Of the 37 recaptures of fish of lower-reach origin (where first tagged), 19 (51%) were more than 10 km from the previous capture site. During the earlier study, such long-distance (L-D) movements comprised 58% of the recaptures. During the recent period, 12 of the 19 (63%) L-D movements were in an upstream direction compared with 68% during the earlier study. These upstream L-D movements averaged 114.1 km (SE = 82.4) whereas the downstream L-D movements averaged 48.9 km (SE = 26.4). Similarly, during the earlier period, the mean distance of upstream L-D movements (108.2 km) was further than the mean downstream L-D movement (35.1 km). Five of the 19 (26%) L-D movements during the recent period resulted in individuals dispersing from the lower reach to the upper reach, a somewhat smaller percentage than during the earlier period (44%). The smallest fish to disperse from the lower to upper reach was between 376 and 434 mm TL when it moved, probably smaller than the smallest fish (421-449 mm TL) to do so during 1991-1995.

For fish first captured in the upper reach during the recent period, 33 of 160 recaptures (21%) were more than 10 km from the previous capture site. Of these, 21 L-D movements (64%) were in an upstream direction. Similarly, during the earlier period, 17% of recaptures represented L-D movements, 75% of which were in an upstream direction. As before, the mean distance of upstream L-D movements (24.9 km ; SE = 8.4) was not significantly different from the mean downstream L-D distance movement (38.1 km; SE = 33.8). However, unlike during the 1991-1995 study, when there were no movements from the upper to lower reach (outside of the spawning period), there were two such movements in the recent period: these individuals moved downstream through Westwater Canyon to locations in the upper 20 km of the lower reach.

Colorado pikeminnow gained access to the Gunnison River upstream of the Redlands Diversion Dam following the completion of a fish ladder at the dam in 1996. Hence, dispersal upstream of the Grand Valley, blocked during the earlier study period, became possible prior to the start of the recent study period. Forty-three different pikeminnow ascended the ladder between 1996 and 2000 (Burdick 2001). Almost all upstream movements through the ladder occurred in July or August (one in early-September), after the mark-recapture sampling was completed for each year. Hence, this emigration from the study area did not violate the assumption of geographic closure for the annual population estimates. Seven of 43 individuals that used the ladder later used it a second time, indicating that they had passed down over the dam sometime after they first ascended (Burdick 2001). In addition, six other individuals that used the ladder were later recaptured downstream of the dam in the lower Gunnison River or in the Colorado River. Only two individuals that used the ladder were later recaptured upstream of the dam, and only one of these in a subsequent year. Hence, the number of fish that have used the ladder and remained upstream of the dam on a permanent basis is unknown. Nevertheless, the fish ladder has effectively connected the Colorado River population with the small remnant population that has persisted in the Gunnison River upstream of the dam (Burdick 2001). On the Colorado River mainstem, upstream dispersal remained blocked at the Price Stubb Dam (rk 303) during both study periods.

Sex Ratio

In the field, gender was assigned to most but not all Colorado pikeminnow captured in 1999 and 2000. For those fish captured when I was not present, sex was either not recorded or, if it was, the results were not included in the analysis[1]. In 1999, I took notes indicating the degree of confidence with each gender determination. These were of three categories: 1) high confidence, 2) medium confidence, or 3) low confidence.

In 1999, I examined 204 captured pikeminnow. These captures included 27 fish that were captured twice, resulting in a total of 178 different fish that were examined. The gender of six (3.4%) of these could not be distinguished. One of the 27 recaptures had a conflicting gender determination on the two dates and was therefore excluded from the analysis; this left a total of 171 sexed fish. Of these, 83 (49%) were identified as females and 88 (51%) were identified as males, suggesting a near 1:1 ratio of males to females. There was generally more certainty surrounding the identification of males than of females: 'high confidence' was noted for 17% of the female identifications and 32% of the male identifications; 'medium confidence' was noted for 40% of the female ID's and 47% of the male ID's; ' low confidence' was noted for 43% of the female ID's and 22% of the male ID's. Part of the reason for males having a higher percentage than females of 'high confidence' identifications was that 39% of the males (11 fish) noted as such were running ripe at the time of capture (13% of all males) whereas no females were similarly running ripe.

In year 2000, I examined 148 captured Colorado pikeminnow. Of these, 135 were different fish (13 fish captured twice). All of these were assigned a gender determination. Sixty-six (49%) were identified as females and 69 (51%) were identified as males. Surprisingly, the percentages of each were in exact agreement with those found for the 1999 captures. Seven males (10%) were running milt when captured.

The male:female ratio found here was consistent with observations made at Dexter NFH with hatchery-reared Colorado pikeminnow. At the hatchery, the sex ratio of nine-year-old

[1]In 1999, gender of four Colorado pikeminnow was recorded when I was not present: two were identified as males and two as females. In 2000, gender of 15 Colorado pikeminnow was recorded when I was not present: nine were identified as males; six as females.

F_1's was 51% males to 49% females (Roger Hamman 2000, personal communication), identical to the ratio observed in the wild during both 1999 and 2000 in the upper Colorado River. Twenty-nine of the 60 fish (1991 F_1 year class) sacrificed at Dexter NFH in 1998 (see Methods) were verified as males (48%) and 31 as females (52%). The fact that the 1:1 ratio found for young fish of one age-class at the hatchery was the same as that found for wild adults of all sizes and ages strongly suggests a lack of gender-selective mortality in the wild, i.e., the ratio holds as fish age.

Until now, the sex ratio of wild Colorado pikeminnow has been a subject of much conjecture. Due to disparate empirical data from spawning bar surveys, Lentsch et al. (1998) used a vote of biologists at a population workshop to arrive at a male:female ratio of 4.5:1. Similarly, U. S. Fish and Wildlife Service (2002a) used a 3:1 ratio, based on the earlier work of Lentsch et al. (1998). One source of uncertainty is whether the ratio in the population reflects the ratio of actual spawners. Tyus (1990) reported non-migratory behavior in 18% of Colorado pikeminnow radio-tracked during the spawning season in the Green and Yampa rivers and attributed it to either non-annual spawning or sexual immaturity. Non-annual spawning, if real, could cause unequal sex ratios at the spawning grounds if males and females had unequal rates of non-annual spawning. However, the non-annual, spawning-migration hypothesis has not been supported by subsequent research: Irving and Modde (2000) reported that all 12 of their radio-tagged Colorado pikeminnow from the White River underwent spawning migrations, not only in one year, but in two consecutive years, in direct contradiction to the non-annual-spawning hypothesis. Earlier observations of non-migratory behavior in some radio-tagged Colorado pikeminnow might be explained by immaturity, as suggested by Tyus (1990), by fish spawning at nearby sites, or by physiological stress resulting from recent radio-tag surgery.

Although behavior at the spawning grounds could also influence the sex ratio of actual breeders, no data or observations exist that would suggest that one gender has a greater rate of spawning success than the other. Thus, for now, the 1:1 sex ratio of the population could be assumed to represent the ratio of breeding adults as was assumed for humpback chubs (*Gila cypha*) by the U. S. Fish and Wildlife Service (2002b).

Sex ratio determination is necessary for population viability analysis. It is one variable that must be considered when estimating an adult population size necessary (N_g) to assure an effective population (N_e) size of 500 or more, currently believed necessary for maintaining long-term genetic variation (Franklin 1980, Rieman and Allendorf 2001). With a 1:1 sex ratio, the effective population size (N_e) equals the number of breeding adults (N_b). Hence, to achieve an N_e of 500, 250 breeding males and 250 breeding females are required. However, it is generally assumed that, for one reason or another, not all individuals within a population of adult fish actually contribute genes to the next generation in a given year, and actual adult population size must therefore be large enough that the subset of the population consisting of individuals actually contributing genes will equal 500 or more. Unfortunately, the average proportion of adult Colorado pikeminnow that actually contribute genes annually is not known. Hence, the actual population size necessary to assure a subset of 500 or more breeding individuals cannot be ascertained with any degree of confidence at this time (estimates of effective/actual population size vary from 0.01 to 0.9 among salmonid species alone [summarized in Lentsch et al. 1998]). Nevertheless, the determination of the sex ratio, presented here, reduces the uncertainty of at least one element that previously hampered efforts to accurately estimate N_g.

Growth Rate

All fish

When the new growth-increment data from 1998-2000 was combined with the earlier data, mean annual increments for each length-class were recalculated. For some length classes, these means increased from the earlier values while others decreased (Table 3); however, most changes were not statistically significant. The most notable change was for the 600-649 mm length-class, where the mean significantly increased from 8.7 to 16.4 mm per year ($P < 0.05$; t-test); also, the mean annual increment of the 800-849 mm-length-group significantly increased from 2.7 to 6.6 mm. By incorporating these new results the growth curve previously reported by Osmundson et al. (1997) changed to some degree (Fig. 9). Adults are still calculated to arrive at 650 mm at an average age of 20 years; at 700 mm at an average age of 23 years; at 800 mm at an average age of 33 years. However, for fish to attain

Table 3. Estimated annual growth increments for Colorado pikeminnow 400 mm total length (TL) and longer in the Colorado River. Mean increments are from measured changes in length of recaptured fish. Length-class is of fish at first capture (year *i*). A combined average increment for fish 550-899 mm TL is also shown because mean increments among these sizes were not significantly different. For fish 400-699 mm TL, increments used in analyses were from capture-recapture measurements one year apart; for larger fish, all capture-recapture increments were used regardless of length of interval. For multiple-year intervals, the growth increment was first divided by the number of years separating captures. Means from the previous analysis (Osmundson et al. 1997) are provided (in parentheses) for comparison.

Length -class at year *i*		Growth from year *i* to year *i* + 1 (mm)		
(mm)	N	Mean (old mean)	Range	SD
400-449	7	41.0 (42.7)	26-60	11.5
450-499	16	25.8 (30.1)	5-68	16.4
500-549	20	14.4 (19.8)	4-35	8.5
550-599	31	9.3 (9.5)	0-31	7.7
600-649*	25	16.4 (8.7)	0-38	11.7
650-699	10	14.3 (12.5)	3-31	8.8
700-749	4	10.9 (14.0)	8-16	3.5
750-799	4	12.1 (10.4)	10-14	1.9
800-849*	8	6.6 (2.7)	0-18	6.2
850-899	4	7.3 (5.1)	2-16	5.9
900-949	3	5.5 (- -)	3-7	2.0
550-899	89	11.6 (9.5)	0-38	9.2

* Length-classes for which the old and new mean increments are significantly ($P < 0.05$) different.

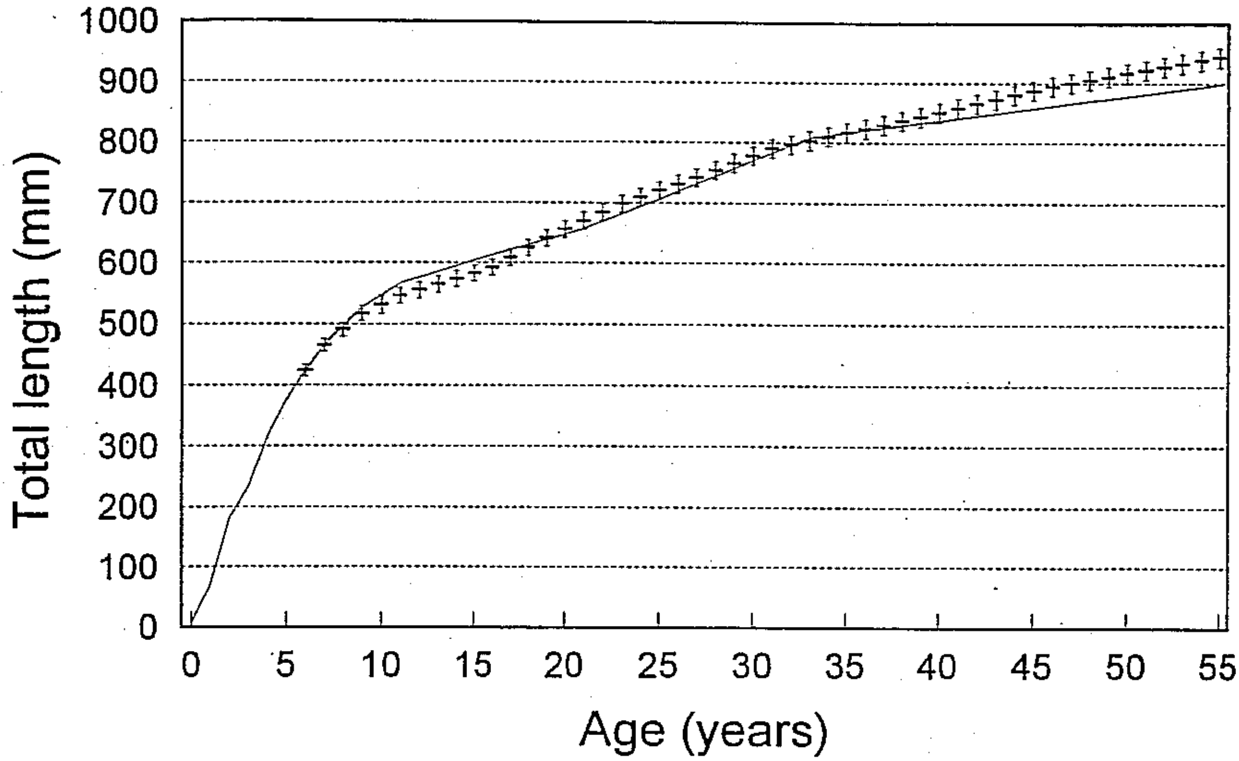

Figure 9. Growth curve of Colorado pikeminnow calculated from revised annual growth increments (see Table 3). Solid line represents curve calculated from previous annual increment data (see Osmundson et al. 1997). Both curves rely on scale aging through mean length of 424 mm. Bars represent +/- 1 SE.

900 mm, the recalculated growth curve indicates it takes an average of 47 years rather than the previously estimated 56 years.

However, results of this growth curve, first reported by Osmundson et al. (1997) and recalculated here, are misleading because of an important assumption the technique is based upon: developing a growth curve for the population as a whole assumes that variation in growth among fish occurs at the individual level only and is not systematic among subsets of the population. This assumption allows the pooling of data from all fish making the calculation of a mean age at a given length possible for the population as a whole. However, if subsets of the population grow faster or slower than others, then a mean age will be erroneous for each subset.

Gender-specific

The most obvious possibility for differential growth rate among subsets of the population is that between the sexes. To date, the literature on this subject has been confusing. Jeppson and Platts (1959) reported that, for northern pikeminnow (*P. oregonensis*), males grew slower than females. However, Vanicek (1967), who used scales to estimate annual growth increments of Colorado pikeminnow, reported that, "no difference in growth between sexes was observed." Tyus (1991) reported that the larger mean size of females compared to males captured at spawning sites of the Green-Yampa river system supported the idea that "females grew larger and perhaps older than males". For females to grow older, they would need a higher survival rate than males. However, Tyus and Karp (1989) suggested that the high ratio of males to females (5:1) captured at spawning sites was evidence of differential survival rates between the sexes, inferring that males have higher survival rates than females. Our data, presented here, however, indicate that the population sex ratio is essentially 1:1. Thus, skewed ratios noted at spawning sites are likely artifacts of sampling bias. For instance, males may stay longer than females at spawning sites, and a larger proportion of the male population is therefore represented there at any one time. Gender-based differential mortality evidently does not occur, as noted above, because the 1:1 ratio exhibited by young fish (hatchery) is maintained when all age classes (wild) are analyzed.

To verify whether females are indeed larger on average than males, the size frequency of males and females in the population was examined using the 1999 and 2000 capture data, for which gender identifications were available. As previously described, fish were sampled from throughout the Colorado River prior to the initiation of spawning activity; hence, any biases associated with spawning site surveys (differential age at maturity, etc.) were avoided. The analysis resulted in a bi-modal histogram, with numbers of males peaking in the 550-599-mm length-class and numbers of females in the 650-699-mm length-class (Fig. 10). The histogram also revealed that females may attain larger sizes than males: individuals identified as females were as large as 965 mm TL, whereas the largest fish identified as a male was 781 mm TL. The largest verified male (running ripe) from the Colorado River was a 697-mm-long individual captured in 1992. Tyus (1990) similarly reported the largest running ripe male from the Green-Yampa system as 735 mm TL. Hence, females are not only larger than males on

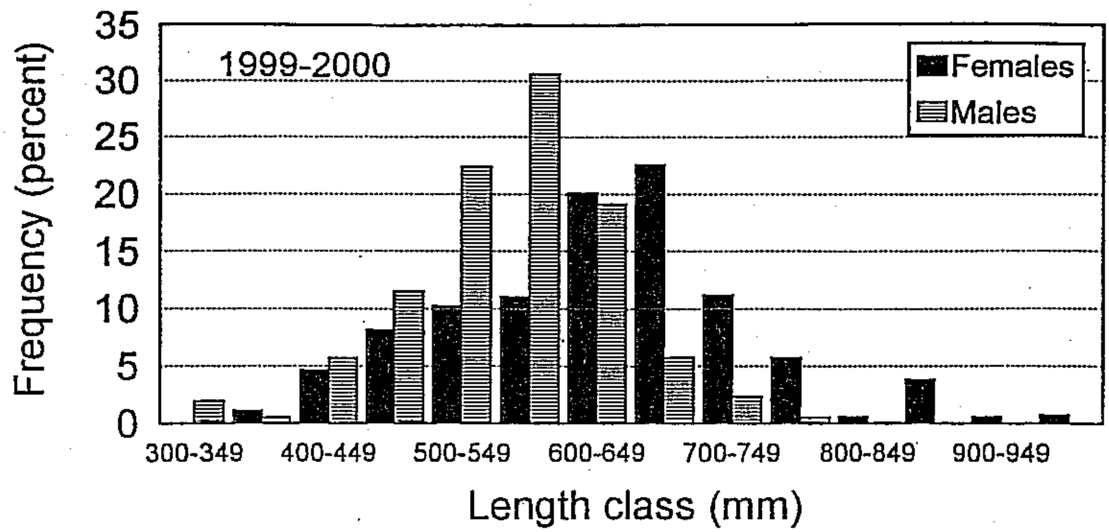

Figure 10. Length-frequency histogram of male and female Colorado pikeminnow captured river-wide in 1999 and 2000.

average but they can also attain larger sizes than males. However, there is little evidence that females live longer than males and the consistency of sex ratios strongly suggests an absence of gender-based differential mortality. These finding lead to the conclusion that gender-based differences in size are due to differences in growth rate alone.

When individual growth increments were averaged by gender, the mean annual growth increment of females was consistently greater than that of males for fish larger than about 450 mm TL (Table 4). However, because of large variation among individuals and relatively small sample size within size classes, not all differences were statistically significant at the 0.05 level: for fish 450-499, $P = 0.27$; for fish 500-549, $P = 0.31$; for fish 550-599 TL, $P = 0.04$; for fish 600-649 TL: $P = 0.02$; for fish 650-699 TL: $P = 0.001$. Thus, for fish > 550 mm TL, mean annual increments of females were significantly greater than for males. Although there is little field-derived increment data for smaller individuals, hatchery-based evidence suggests gender-based differences in growth rate may begin in Colorado pikeminnow smaller than 450 mm TL. At Dexter NFH in 1999, 60 1991 F_1 Colorado pikeminnow were sampled, measured for total length, and sacrificed to verify gender. Total length of these ranged from 338 to 484 mm TL. Mean length of females (408 mm) was significantly greater ($P = 0.01$; two-sample t-test) than that of males (389 mm), suggesting that female growth rate may exceed male

Table 4. Estimated annual growth increments for male (M) and female (F) Colorado pikeminnow 400 mm total length (TL) and longer in the Colorado River. Mean increments are from measured changes in length of recaptured fish. Length-class is of fish at first capture (year *i*). Sample sizes (N) for length classes differ from those listed in Table 3 because of different inclusion criteria (see Methods).

Length-class at year *i*			Growth from year *i* to year *i* + 1 (mm)		
(mm)	Sex	N	Mean	Range	SD
400-449	M	2	41.5	23-60	26.2
	F	4	38.1	26-56	13.9
450-499	M	9	19.9	9-39	10.6
	F	4	26.8	18-33	6.5
500-549	M	33	12.0	1-35	6.6
	F	6	17.5	5-39	11.7
550-599*	M	24	8.0	0-41	8.9
	F	14	15.0	3-33	9.9
600-649*	M	17	9.9	0-31	7.9
	F	21	18.2	0-38	11.6
650-699*	M	3	3.9	3-6	1.5
	F	9	19.7	14-31	6.0
700-749	M	0			
	F	3	11.8	9-16	3.7
750-799	M	0			
	F	4	12.8	10-14	2.1
800-849	M	0			
	F	3	6.6	0-13	6.1
850-899	M	0			
	F	3	8.8	5-16	5.8
900-949	M	0			
	F	2	3.5	3-4	0.7

* Length-classes for which mean increments of males and females are significantly ($P < 0.05$) different.

growth rate before a length of about 450 mm is attained. For wild fish 450-550 mm long, I assumed then that, although differences between gender were not statistically significant, the mean increments calculated for each gender were probably reasonable approximations of average annual growth increments; I therefore used the results to develop growth curves specific to each gender.

As before, the curves are based on scale analysis (not gender specific) until fish reach 424 mm TL, and assume equal growth between sexes until 450 mm, the first size (450-499 mm size-class) with sufficient data to show differences in average annual increment. However, the hatchery results outlined above suggest that divergence in growth might occur earlier and therefore the curves presented here may be inaccurate to a small degree. Additionally, the curve for males is extended to age 55 (770 mm TL) based on extrapolation of mean increments of males 650-699 mm long because there was insufficient data points to calculate mean increments for males in the 700-749 or 750-799 mm length-classes.

The two curves indicate a clear divergence in growth resulting in females attaining a larger size than males, as expected (Fig. 11). Also, the curves indicate that it takes an average of 14 years for females to reach a length of 600 mm, whereas for males, it takes an average of 17 years. More dramatically, females may grow to 700 mm TL in 19 years whereas males would require an average of 33 years. The earlier, non-gender-based growth curves indicated that for pikeminnow to reach 900 mm in length, an average of 56 years (Osmundson et al. 1997) or 47 years (this study) was required; however, the gender-based curves revealed that such a length would be attained by females in 39 years and that males simply do not reach such lengths.

The 965-mm-long female Colorado pikeminnow captured from the Colorado River in 2000 would have been 54 years old when caught if it grew at the estimated rate for females; however, it could have been younger if it grew faster than average. Similarly, the 781-mm-long individual identified as a male may have been younger (or older) than the estimated age of 53 years.

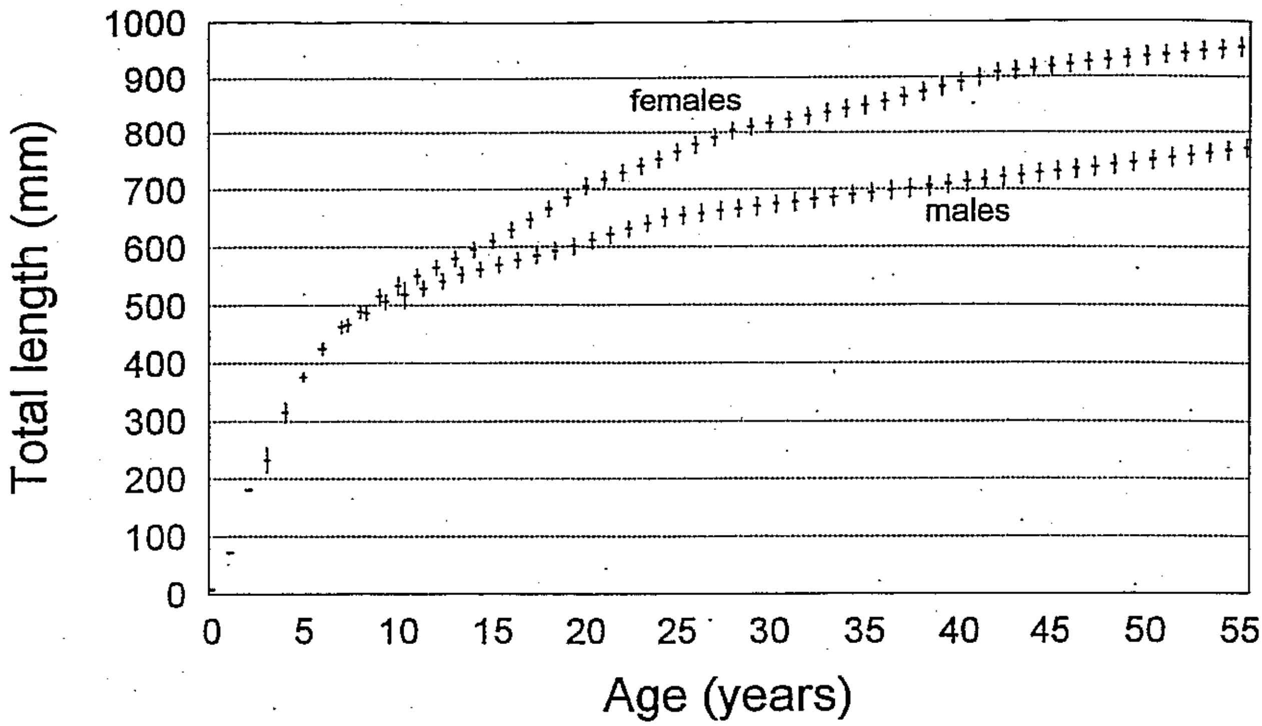

Figure 11. Growth curves of male and female Colorado pikeminnow calculated from gender-specific annual growth increments (see Table 4). Curves assume equal growth rate up until 450 mm in length. Both curves rely on scale aging through mean length of 424 mm. Bars are +/- 1 SE.

Body Condition

Average physical condition of Colorado pikeminnow declined between the early (1991-1994) and recent (1998-2000) sampling periods in both the upper and lower reaches (Fig. 12). Osmundson et al. (1998) documented how average body condition in the lower reach declined as mean length increased, whereas in the upper reach, body condition increased with increased length. This pattern was still evident in the recent period. However, mean relative body condition (*Kn*) of fish within all size classes was lower in the recent period than for the same size classes in the earlier period. In most cases, these declines were statistically significant (P = 0.05) as determined by ANOVA. The only exception in the lower reach was for 600-699-mm-long individuals, evidently due to low sample size (n = 7 and 9). In the upper reach, declines in

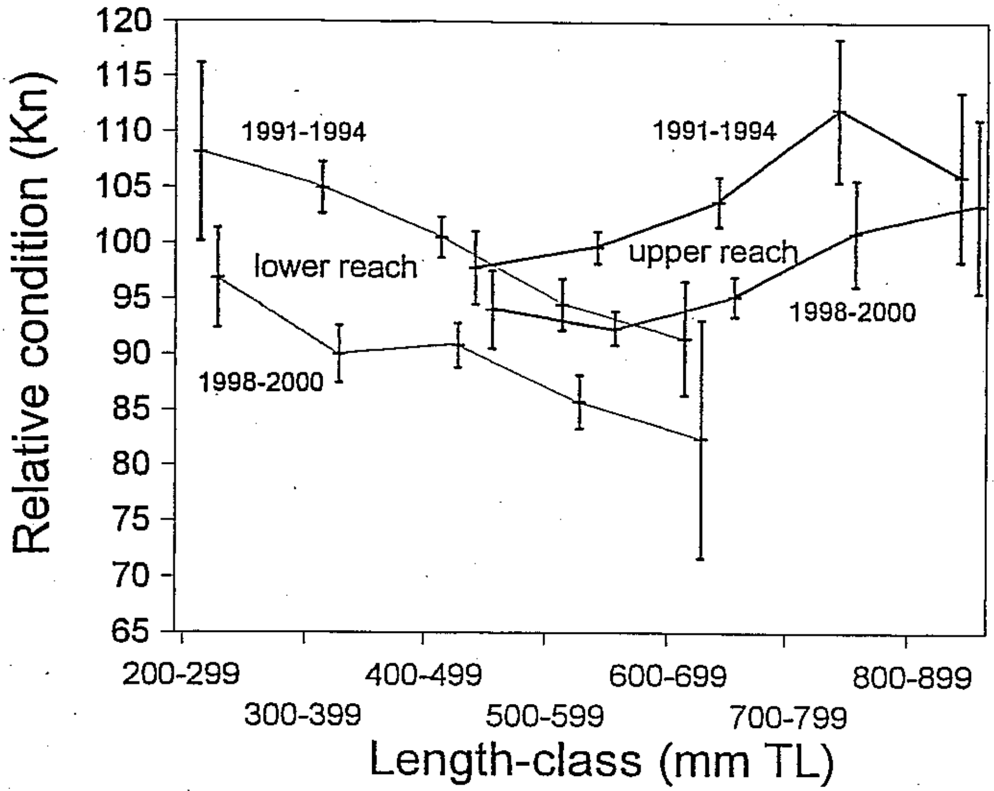

Figure 12. Mean relative condition of Colorado pikeminnow by length-class, study reach, and study period. Error bars represent 95% confidence intervals.

relative condition of Colorado pikeminnow 400-499 and 800-899 mm long were also not significant.

Because body condition not only varies by length-class, but also by reach, temporal changes are best examined by keeping length-class constant and separating results by reach. Hence, to keep size constant, comparisons were made using fish 500-599 mm long. This length-class was best suited for this because: 1) it was the only length-class for which sample size was large in both the upper and lower reach, and 2) all fish of this size are assumed to be adults. Results from ANOVA indicated significant differences ($P = 0.000004$) among years in the upper reach for fish 500-599 mm long: although mean condition was not significantly different ($P > 0.05$) among years within study periods (1991-1994 and 1998-2000), mean condition in all three recent years (1998, 1999 and 2000) was significantly lower ($P < 0.05$) than in all four earlier years (1991, 1992, 1993 and 1994). For the lower reach, ANOVA also indicated significant differences ($P = 0.000000$) among years. Like the upper reach, no

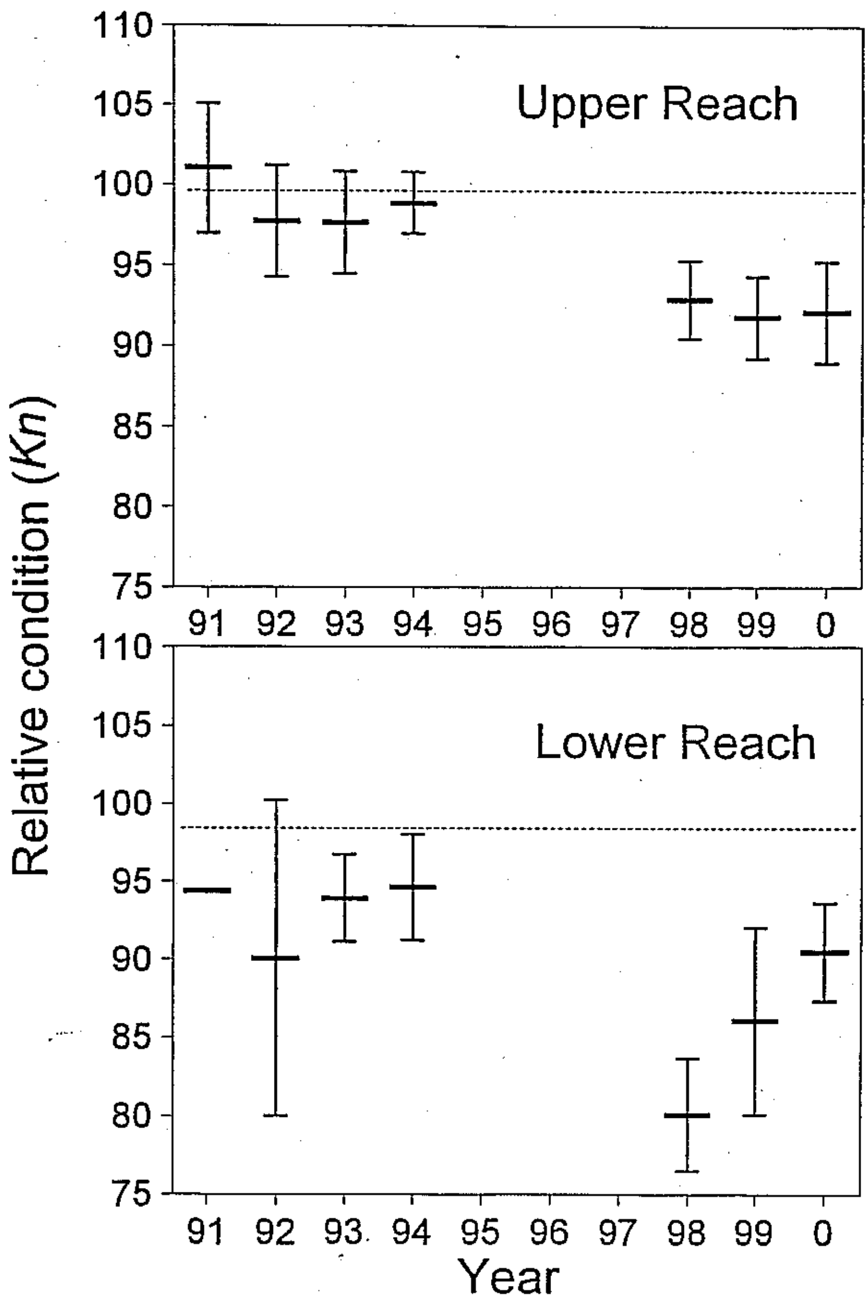

Figure 13. Annual mean relative body condition of Colorado pikeminnow 500-599 mm long in the upper (top) and lower (bottom) reaches. Error bars represent 95% confidence intervals.

significant differences ($P < 0.05$) were found among years of the early period; however, not only was there a drop in condition from the end of the early period to the beginning of the recent period, but there was a distinct upward trend in condition from 1998 to 2000 (Fig. 13). Mean condition in 1998 was significantly lower ($P < 0.05$) than in 1992, 1993 and 1994.

Condition was also significantly lower in 1999 than in 1993 and 1994. However, by year 2000, mean condition was significantly higher than in 1998 and was not significantly different ($P > 0.05$) than in any of the earlier years of 1991-1994.

Next, among-year comparisons for the recent period were made for upper-reach fish 600-699 mm long. This length-class made up an important component of the female sub-group during the years for which there were gender identifications (1999 and 2000). Lowered condition might be important if it affects quantity or size of eggs produced. To see if condition varied by gender, condition of males and females from 1999 and 2000 were compared: ANOVA indicated no difference ($P = 0.407$) in condition between the sexes (Mean *Kn* of males: 96.2; mean of females: 94.4). Therefore, data from both males and females were used to compare mean condition between 1999 and 2000. ANOVA indicated mean *Kn* of pikeminnow 600-699 mm long significantly increased from 93.08 to 97.54 between 1999 and 2000 ($P = 0.046$).

Changes in body condition likely reflect changes in food availability. Increased numbers of predators could crop available forage to the point that prey scarcity affects predator body condition. In a predator density-dependent scenario, if predator numbers decline, prey and predator body condition would theoretically increase. Alternatively, there may be natural variation in prey density due to strong or weak year classes of key forage types; such temporary scarcity of prey may not be acute enough to affect predator numbers but may manifest itself in temporary declines in predator body condition. In this scenario, as strong year classes of prey return, body condition of predators would be expected to improve. Unfortunately, no data on prey abundance (fish < 300 mm TL) were collected that might allow correlations between prey density and body condition of Colorado pikeminnow. Although netting catch rates of sympatric species were recorded, mesh size was selective for larger fish and length data that would allow partitioning of forage-size individuals was not recorded.

Length Frequency

Size structure of the Colorado pikeminnow population is dynamic and shifts in length frequency can provide clues to near-term trends in recruitment. Because recruitment in the upper reach is almost exclusively provided by colonization from sub- and young adults migrating there from the lower reach (see Osmundson et al. 1998), frequencies of small length-classes (< 450 mm) are fairly static and are therefore not particularly instructive in gauging year-class strength. Most young fish rear in the lower reach and it is there that recent year-class strength can be discerned and predictions made regarding future adult recruitment.

In 1991, a large pulse of young fish (300-400 mm TL) was detected in the lower reach which later accounted for a pulse in adult recruitment in the mid-1990s (Osmundson et al. 1998). Estimated ages (scale analysis) of sub-samples of this group indicated three year-classes (1985-1987) with the strongest from 1986. There was much overlap in size among the three year-classes demonstrating the difficulty in using size as a basis for estimating year of origin. However, despite these limitations, the earlier observations provided clues for the interpretation of the more recent size structure results.

Although there was no dramatic pulse of fish in the lower reach as was observed in the early 1990s, there were clearly fish recruiting to the sub- and young-adult phases during the late 1990s. These fish evidently originated from some weak to moderately-strong year-classes produced during 1990-1994. Also, it appears that very little recruitment can be expected from the succeeding 1995 and 1996 year classes because there were very few fish less than 400 mm long in 1999 or in 2000 (Fig. 14). Curiously, abundant YOY produced in 1996 (see Fig. 15) never materialized as a strong year class. By 2000, these fish, at four years old, should have averaged 315 mm (Osmundson et al. 1997), and therefore would have been susceptible to trammel netting as well as electrofishing. The fact that no pulse of this size fish was detected suggests that high YOY numbers may not always guarantee high recruitment in later years.

In the upper reach, estimating age based on size becomes even more difficult than in the lower reach because growth rate of Colorado pikeminnow slows when individuals reach adult size, i.e., fish of many year classes tend to stack up in the 500-549 and 550-599 mm length-classes. However, some observations may be made from the upper-reach, length-frequency histograms. In 1993 and 1994, about 15% of the population was made up of fish in the 450-499 mm length-class, evidently recent migrants from the lower reach (see Osmundson and Burnham 1998). In 1998-2000, this length-class made up only 3-7% of the population (Fig. 16). Additionally, the length-class making up the greatest proportion of the upper-reach fish

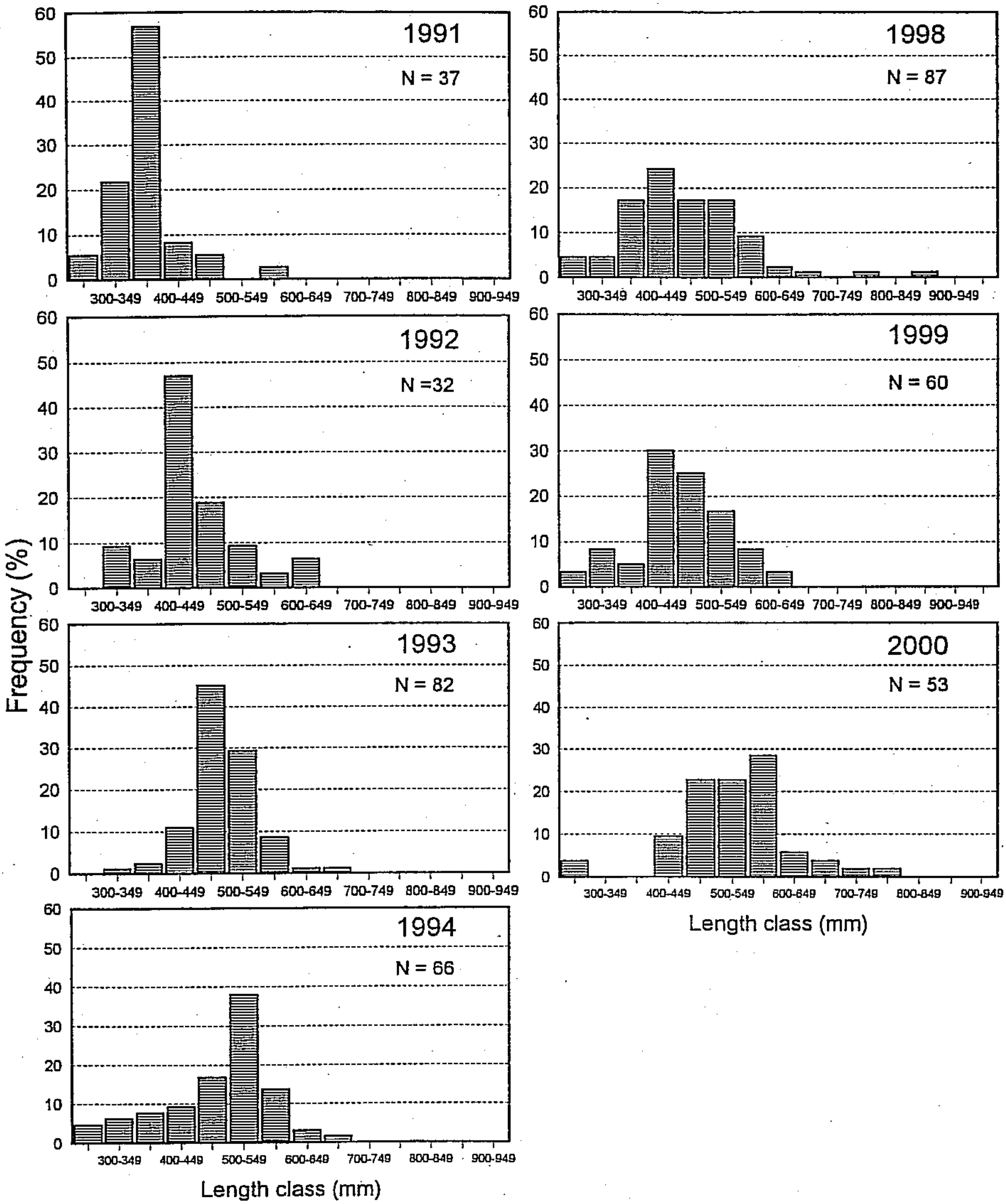

Figure 14. Annual length-frequency of Colorado pikeminnow captured in the lower reach during early and recent study periods.

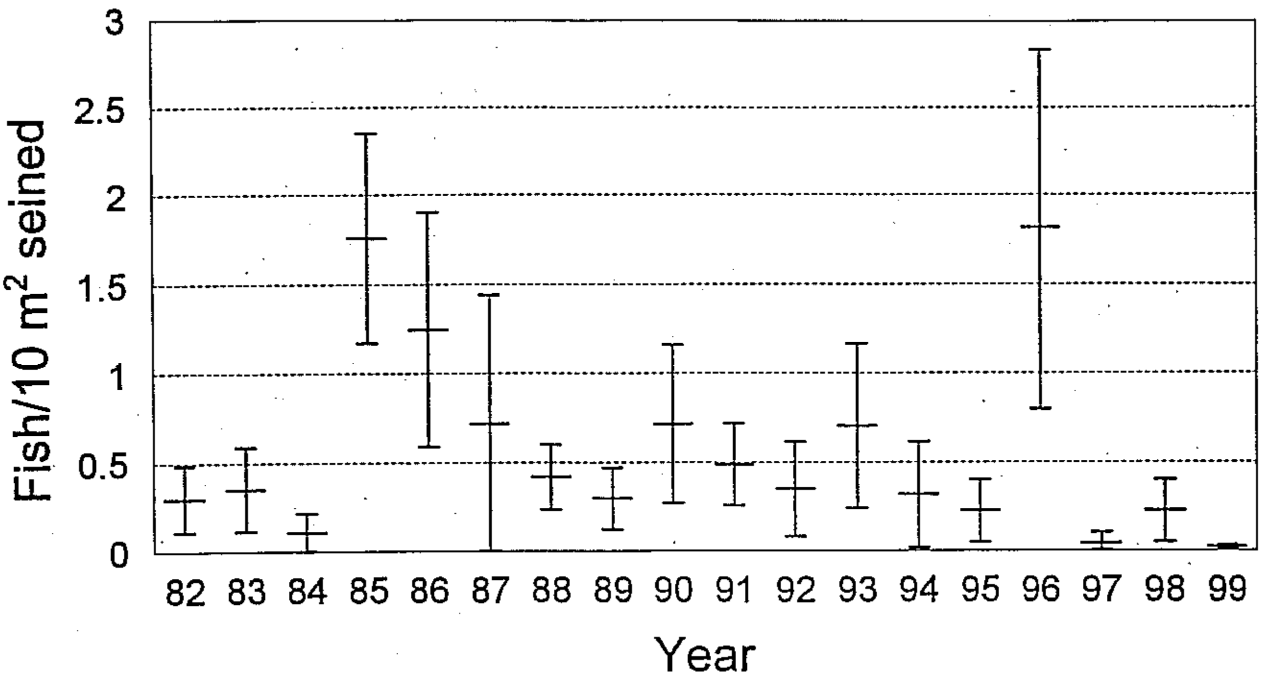

Figure 15. ISMP annual catch rates of young-of-the-year Colorado pikeminnow seined from backwaters during fall. Interagency Standardized Monitoring Program data summarized and provided by Charles McAda (USFWS).

shifted from the 550-599-mm-length-class (1991-1994) to the 600-649-mm-length-class (1998-2000). This can best be seen when the data from the annual histograms are pooled by period (Fig. 17). Fish ≥ 600 mm made up 56% of the population in the recent period compared to 40% in the prior period. These results reveal a population consisting of a greater percentage of large, older adults, representing the "baby-boom bubble" produced in the mid-1980s continuing to work its way up through the age classes.

Predicting Change in Adult Numbers

The average annual growth increment of 25.8 mm for fish 450-499 mm long was used to calculate a minimum length of 474.2 mm in year *i* for fish expected to recruit to 500 mm or longer in year *i* + 1 (500 - 25.8 = 474.2). Results of the exercise indicate a substantial increase in adults (38%) between 1993 and 1994 (Table 5). Unfortunately, there were no data to calculate results for the 1995-1996, 1996-1997, and 1997-1998 periods. In the recent period, the method estimated adult losses of 10% during 1998-1999, 4% during 1999-2000, and

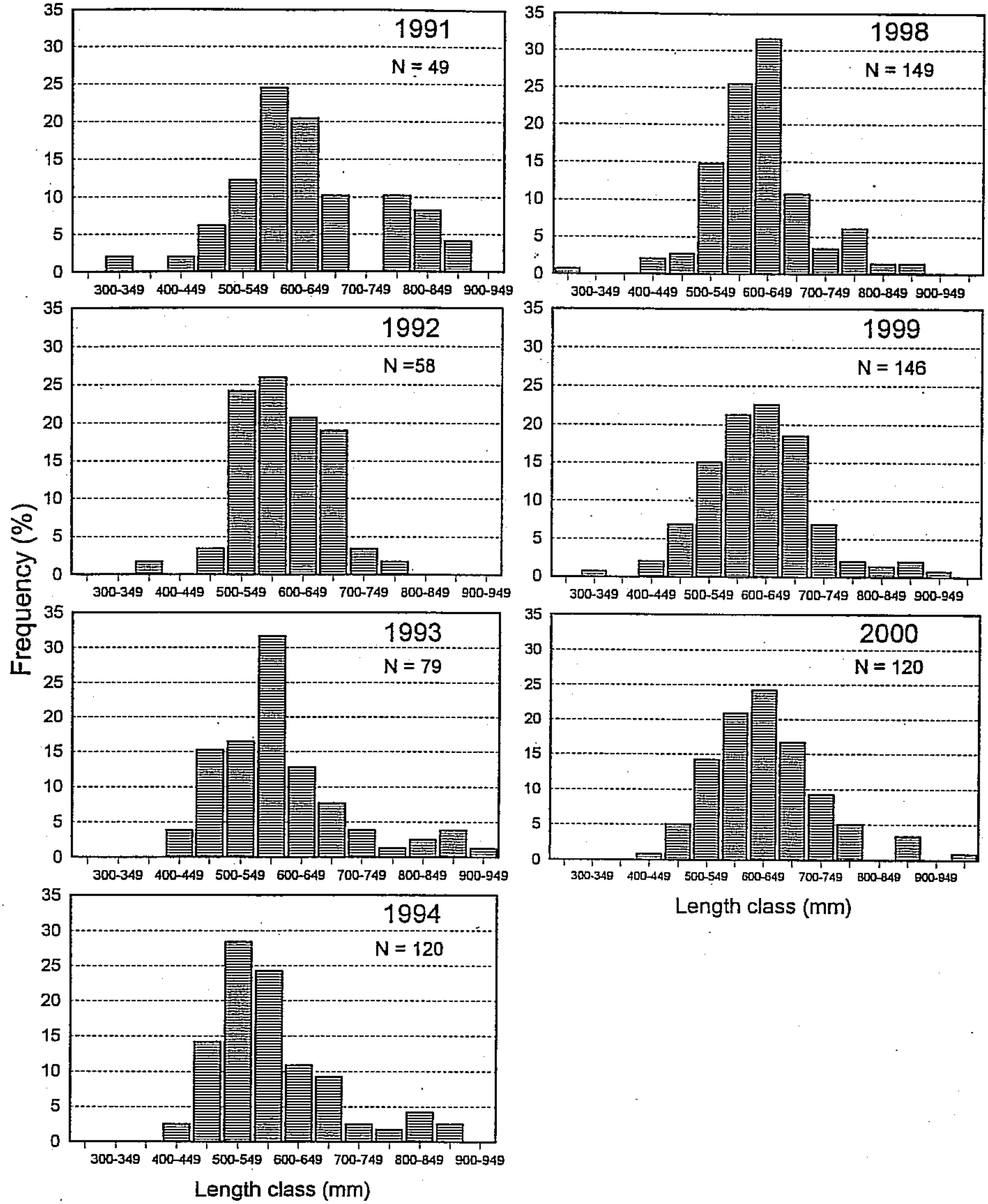

Figure 16. Annual length-frequency of Colorado pikeminnow captured in the upper reach during early and recent study periods.

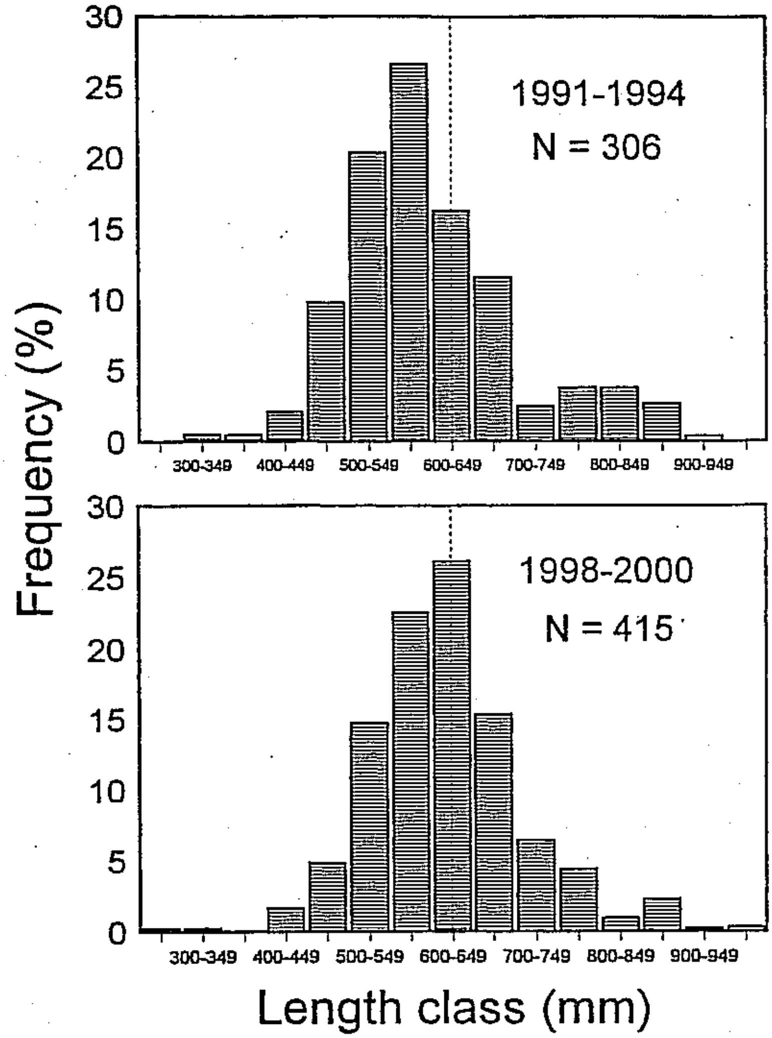

Figure 17. Length-frequency of Colorado pikeminnow captured in the upper reach during early (top) and recent (bottom) study periods with multi-year data pooled by period.

essentially no change from 2000 to 2001.

It is important to note that the abundance point estimates play a large role in these calculations. The point estimates are values the mark-recapture models calculate based on the data provided, but should not be interpreted too literally. The 95% confidence intervals around these point estimates tell us that if the two- or three-pass sampling was conducted 100 times on the same population, 95 of the resulting point estimates would fall within the given interval, which in many cases is quite wide. Hence, a population point estimate derived from our one sampling effort is just one of many possible outcomes.

Table 5. Estimates of annual population increase and decrease of adult Colorado pikeminnow in the Colorado River based on expected recruitment and survival, 1991-1994 and 1998-2000. Survival rate assumes 86%. Year listed is year at time *i*.

	Pop est	Fish 474-499 mm percent	Fish 474-499 mm number	Adult pop est	Survival to yr *i* + 1	Adults at yr *i* + 1	change expected
				1991			
upper reach	215	3.4	7	197			
lower reach	--	0.0	0	(10?)			
Whole river total			7	207?	178	185	-10.6%
				1992			
upper reach	381	4.6	18	316			
lower reach	151	18.2	27	8			
Whole river total			45	324	279	324	+0.0%
				1993			
upper reach	163	9.1	15	130			
lower reach	435	27.3	119	125			
Whole river total			134	255	219	353	+38.4%
				1994			
upper reach	368	12.4	46	337			
lower reach	249	13.0	32	170			
Whole river total			78	507	436	514	+1.4%
				1998			
upper reach	441	1.4	6	394			
lower reach	282	5.8	16	113			
Whole river total			22	507	436	458	-9.7%
				1999			
upper reach	356	4.8	17	307			
lower reach	324	6.7	22	91			
Whole river total			39	398	342	381	-4.3%
				2000			
upper reach	463	5.0	23	415			
lower reach	359	15.0	54	149			
Whole river total			77	564	485	562	-0.4%

Several discrepancies were noted: the exercise predicted a 4.3% decrease in adults between 1999 and 2000, while change in population point estimates for this period (Table 2) indicated a 42% increase in adults (398 in 1999; 564 in 2000). A similar discrepancy was found for the 1991-1992 period. Although no river-wide population estimate could be calculated for 1991 because of a lack of a lower-reach estimate that year, size-frequency analysis indicated only 3% of the lower reach group consisted of fish ≥ 500 mm TL. Hence, almost all of the river-wide adult population can be assumed to have consisted of the estimated 197 adults that resided in the upper reach at that time. Thus, the 1991 number of adults increased from around 200 in 1991 to an estimated 324 in 1992, representing a 62% increase. This result is in stark contrast with the 11% decrease in adult numbers predicted from the recruitment-based exercise. Thus, the two methods produced very different results in two of the periods for which there were consecutive-year data to make comparisons. Other discrepancies: for 1992-1993, no change (0%) was predicted versus an estimated loss (based on population point estimates) of 21%; for 1993-1994, a predicted gain of 38% versus an estimated gain of 99%; for 1998-1999, a 10% predicted loss versus a 21% estimated loss. Inaccurate population point estimates likely account for the big discrepancies noted. These estimates not only form the basis in the initial year (to which future recruitment and survival factors are added) for the prediction of population size in the following year, but also provide the number in the subsequent year against which the prediction is compared. Hence, the predictions and our ability to evaluate them are only as good as the accuracy of the point estimates. In addition, the length-frequency histograms may not provide an accurate portrayal of the true proportion of fish about to recruit.

Biologist Sampling Effect

Sampling Colorado pikeminnow for a variety of research and management purposes, including gathering data for this study, has a negative effect on the population. This effect must be acknowledged and weighed against the intended benefits associated with sampling. Direct mortality of some individuals is the most obvious effect, but may or may not be the most important. Other effects may include injury or disruption to reproduction from electrofishing trauma, handling stress, or hazing of fish from preferred habitats.

Gilpin (1993), citing Rich Valdez, suggested that researchers can cause 2% adult mortality. I explored this suggestion by tabulating known researcher-induced mortalities of Colorado River pikeminnow by year from the 1990-2001 pit-tag capture list (Table 6). Mortalities of Colorado pikeminnow ≥ 250 mm TL, including permanent removals, totaled 36, ranged from 0 to 10 individuals per year, and averaged three per year for the 12-year period. Assuming an average annual population size of 662 (average of 1992-1994 and 1998-2000 point estimates), this average annual sampling mortality rate equaled 0.45% of the population. Considering only adults (≥ 500 mm TL), there were 25 known mortalities, averaging 2.1 per year, or approximately 0.49% of the average annual population of 426 adults. Hence, from a long-term perspective, the effect is much lower than the Gilpin estimate. However, there were individual years when the effect was much higher. For instance, as previously reported here, there may have only been about 200 adults throughout the river in 1991. In the prior year, 1990, nine individuals > 500 mm were removed from the river, or about 4.5% of the adult population. Known losses from sampling are not included when natural survival and mortality rates are calculated from open-population mark-recapture models, so these losses are in addition to the 14-15% estimated mortality rate (see Osmundson et al. 1997 and Osmundson and Burnham 1998).

During the 12-year period, there were several types of research or management activities that resulted in direct losses of fish (Table 6); of these, propagation-related projects had the greatest impact. Fifteen of the 25 adult mortalities (60%) were associated with propagation. As previously mentioned, nine adults (and one < 500 mm) were removed from the river in 1990 for broodstock use at Dexter NFH. While at the hatchery, eight of these died. The remaining two were returned to the Colorado River in 1992; these two evidently did not survive because they were never captured again despite intensive sampling. In 2000, 13 wild pikeminnow captured during the population estimation study were moved to the endangered fish facility at Horsethief State Wildlife Area (SWA); six of these (46%) died within two weeks. One died in a similar attempt to spawn wild fish at Horsethief SWA in 1999. In both cases, no captive fish were successfully spawned and survivors were released. Besides propagation, population estimation sampling (this study) resulted in the most mortalities: a

Table 6. Colorado River annual pikeminnow mortalities associated with Recovery Program activities, 1990-2001. Numbers include pikeminnow ≥ 250 mm TL.

	Year											
Activity	90	91	92	93	94	95	96	97	98	99	00	01
Radiotelemetry				3								
Propagation	10									1	6	
Population estimation		5	1						2	2		
Translocation												4
Misc surveys							1	1				
Total	10	5	1	3			1	1	2	3	6	4

total of 10 Colorado pikeminnow died in trammel nets during the seven years of intensive sampling. Of these, seven were < 375 mm long. These smaller individuals died because they became 'gilled' in net mesh while in very warm water and could not be removed fast enough. Additionally, a translocation study that had 19 Colorado pikeminnow moved from the Grand Valley to the De Beque-to-Rifle reach in 2001 resulted in the death of four adults after they became trapped in the Government Highline Canal (B. Burdick, unpublished USFWS data).

Delayed mortalities are another source of concern. These occur when fish experience severe trauma from netting or electrofishing injury, or are stressed from being temporarily held in captivity and repeatedly handled; they are alive when released but ultimately do not recover from the experience. Delayed mortalities are suspected but not confirmed; hence, occurrence is impossible to quantify. Individuals that bleed from the gills following electrofishing are candidates for delayed mortality. Severe entanglement in trammel nets can sometimes clamp shut the opercles of large individuals for prolonged periods; this can starve the fish of oxygen and perhaps cause irreparable harm even though the fish is still gilling when released. Unlike direct mortalities, the occurrence of delayed mortalities, though unknown, is automatically included in mark-recapture estimates of mortality rates.

Non-fatal injuries are more common than sampling-related deaths and the effect of such injuries on fish health is unknown at both the individual and population level. Skin abrasions are common and caudal fins are often split apart from net-mesh entanglements. Whether these injuries later result in secondary infections is unknown. Certainly, many fish survive fairly grievous wounds, including those from heron-beak punctures, expelled radio-tags, etc.

In addition to physical injury, the effect of sampling on fish physiology or behavior is unknown. Clearly, netting and motoring within every backwater 2-3 times a season is disruptive to endangered and other fish that seek these sites as refuges from high main-channel flows. Disruption to these sites and repeated capture and handling of individuals may result in them being hazed from preferred or essential habitats.

Of equal or greater concern is the effect electrofishing may have on Colorado pikeminnow spawning success. Shocking of ripe females immediately prior to spawning significantly reduced egg hatching rates of chinook salmon (Cho et al. 2002) and razorback sucker (Muth and Rupert 1996). For Colorado pikeminnow population estimates, sampling is generally completed prior to the spawning season and females should not yet be ripe at the time of capture. However, there have been exceptions to this. In 1994, runoff ended early in the Colorado River before the completion of the upper-reach third pass in mid June. Because backwaters were no longer flooded, crews electrofished shorelines to capture Colorado pikeminnow; in the process, a spawning site[2] was discovered in the Grand Valley and 10 individuals were captured. Crews returned 1 and 2 wk later and captured nine more with trammel nets. In June 1998, the site was again electrofished to verify its continued use as a spawning site and 12 Colorado pikeminnow were captured. Although such surveys were curtailed, crews returned in 1999 and 2000 to shock spawners for use at the Horsethief SWA facility.

In June 1999, 24 adult Colorado pikeminnow captured from the Grand Valley during

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[2]This site met the criteria of a "confirmed spawning site" as defined in the Rare and endangered Colorado River fishes sensitive area document (Biology Subcommittee 1984): (1) two different radio-tagged Colorado pikeminnow moved to this site during the suspected spawning seasons of 1992 and 1993 (USFWS unpublished data); (2) deep pools interspersed with cobble/riffle habitat occur at the site; (3) a ripe female was collected in 1999 (see text above); and (4) Colorado pikeminnow larvae 7.5-11 mm long were collected (406 total) at a drift station located 16 miles downstream in all years from 1992-1996 (Anderson 1999).

population estimation sampling were transferred to the Horsethief facility. After attempts to spawn these fish were unsuccessful, they were returned to the river. Therefore, in July, 12 Colorado pikeminnow were electrofished from the spawning bar including one running-ripe female; this fish was successfully spawned along with another captured from the 15-mile reach. Electrofishing crews again returned to the spawning bar in 2000 when additional attempts to spawn captive wild fish at the Horsethief facility were unsuccessful; however, no Colorado pikeminnow were captured.

In summary, many Colorado pikeminnow in the Colorado River have been shocked, netted, handled, anesthetized, pit-tagged, transported, held in captivity, injected with hormones, muscle-plugged, etc. During 1998-2000 sampling for this study, 29-40% of the estimated upper reach population was captured and handled annually. Some individuals were handled multiple times; in fact, the very nature of mark-recapture studies necessitates this. What effect this has on reproductive physiology is unknown and is of particular concern given that most sampling occurs 1-2 months prior to the spawning period at a time when fish are becoming physiologically ready for migration and spawning. Clearly the information gained from mark-recapture studies has been essential to furthering our understanding of life history traits and population status. Artificial propagation efforts that include temporarily removing adults from the wild spawning population as well as electrofishing spawning bars is clearly disruptive and likely results in lowered larval production and reduced effective population size (N_e). Given that inadequate reproduction and recruitment rates were identified by Osmundson and Burnham (1998) as primary limitations to population viability in the Colorado River, the benefits accrued from scientific studies and artificial propagation efforts must be carefully weighed against the detrimental effects associated with sampling.

SYNTHESIS

Abundance of Colorado pikeminnow in the upper Colorado River increased during the 1990s. In 1991, the first year of mark-recapture population estimates, only a remnant population existed, apparently including no more than about 200 adults. However, high spring flows in the mid-1980s laid the groundwork for a series of successful year-classes (McAda and Ryel 1999) which later recruited to the adult population in the early- to mid-1990s (Osmundson and Burnham 1998). By 1998-2000, annual estimates averaged 490 adults. Hence, given the proper environmental conditions, the population proved capable of substantially rebuilding its numbers through natural reproduction and recruitment.

Capture-recapture population estimation techniques have allowed better tracking of population dynamics. Although catch-rate results provide only an index to population trends and not to absolute abundance, the trends they reveal provide a valuable consistency check on trends revealed by the population estimates. Other ancillary information, such as dispersal and body condition results, also provide clues to trends in population dynamics. To best discern trends, all sources of information and lines of evidence should be utilized to build a cohesive interpretation of population dynamics. Based on the population estimates alone, we might conclude that the adult population continued to increase throughout both study periods. However, although other data support the overall trend, there is some evidence that numbers may have actually declined rather than increased during the last three years of study, 1998-2000. These other lines of evidence are discussed below.

Netting catch rates in upper-reach backwaters support the conclusion that the population substantially increased in number between 1991 and 1993. This was also supported by ISMP electrofishing results which first displayed a marked increase in upper-reach catch rates in 1991 and lower-reach catch rates in 1992. Population point estimates and backwater-netting catch rates also indicated that the number of Colorado pikeminnow increased between 1994 and 1998. Trends in body condition, although difficult to interpret, may also lend support to the possibility of an increasing population during this time. If food is limited for this predator, lowered body condition would be an expected result of increased intraspecific competition following the addition of more Colorado pikeminnow to the population. There was a significant decline in mean *Kn* for almost all length-classes of Colorado pikeminnow between the 1991-1994 and 1998-2000 periods in the upper reach coinciding with increased abundance. Lowered condition is symptomatic of food limitations. However, decreased food availability may result from either higher rates of predation from an increasing Colorado pikeminnow population or a decline in food production, or both. For instance, in the lower reach, body condition declined but point estimates, netting catch rates, and electrofishing catch rates (ISMP) indicated that the number of Colorado pikeminnow did not change significantly between 1994 and 1998. Hence, lowered body condition there, particularly during 1998, may have resulted from a decrease in forage production rather than an increase in Colorado pikeminnow. Declines in body condition therefore must be interpreted cautiously. Assuming increased competition, a decline in mean *Kn* for the upper reach between 1994 and 1998 was supportive of other results that suggested the population increased.

During 1998-2000, population point estimates in the upper reach varied somewhat among years but the differences were not statistically significant. There was more variation in the netting and ISMP electrofishing catch rates; however, differences among years were also not significant. Body condition of Colorado pikeminnow 500-599 mm TL was reduced but remained steady during these years. These lines of evidence suggest that abundance in the upper reach remained relatively steady during the 1998-2000 period.

However, other evidence suggests that competition for food among Colorado pikeminnow may have decreased between 1998 and 2000, either from a reduction in Colorado pikeminnow or perhaps an increase in their food supply. Body condition of upper-reach Colorado pikeminnow 600-699 mm long significantly increased between 1999 and 2000. Emigration from the Colorado River to the Gunnison River via the Redlands Fish Ladder tapered off in 1999 and 2000 (4-5 individuals used the ladder each year) after numbers using the ladder peaked at 18 in 1997 and 23 in 1998 (Burdick 2001). Emigration may be viewed as a response to intraspecific competitive pressure. A reduction in emigration and an increase in body condition of the larger individuals suggests food resources in the Colorado River may have improved by year 2000. Despite these results, which are difficult to interpret, the safest conclusion at this time appears to be that Colorado pikeminnow numbers in the upper reach were relatively stable during the 1998-2000 period.

In the lower reach, the various 1998-2000 results were more contradictory than in the upper reach. Abundance point estimates indicated that total numbers, as well as adult numbers, increased from 1998 to 2000. Yet, netting catch rates significantly declined between 1998 and 1999, and ISMP electrofishing catch rates also significantly declined between 1998 and 2000. Mean body condition of individuals 500-599 mm TL significantly increased in the lower reach between 1998 and 2000 suggesting a reduction in intraspecific competition, either from an increase in forage production or a reduction in Colorado pikeminnow numbers (or both). Individuals continued to disperse from the lower to the upper reach but at rates slightly lower than during the early 1990s, and two fish even returned to the lower reach after first migrating to the upper reach.

The lower-reach capture-recapture point estimate in 1998 was based on six recaptures and the confidence interval was reasonably narrow. However, there were only two recaptures in 1999, and only one in 2000. Although program CAPTURE can calculate a point estimate with such low recapture rates, results are not very reliable. Hence, based on all lines of evidence, it is likely that the total number of Colorado pikeminnow in the lower reach actually declined from 1998 to 2000 despite point estimate results that indicated an increase. However, length-frequency revealed a higher percentage of adults compared to juveniles and subadults (250-499 mm) in the lower reach in 2000 than in the preceding two years, and although total numbers may have declined there, adult numbers may have actually remained fairly constant. Estimates from years with low recapture rates should be treated with caution, underscoring the importance of averaging estimates over a three-year period rather than putting too much faith in individual annual point estimates.

In addition to allowing the monitoring of trends in population abundance, the intensive capture efforts made during this study provided important ancillary data that has improved our understanding of Colorado pikeminnow life history. The finding of a 1:1 sex ratio in the population brings us a step closer to ascertaining an accurate estimate of the number of adults needed to provide an effective population (N_e) size of 500. Gender-specific growth rate, also reported here, provides a whole new insight on Colorado pikeminnow growth, and helps refine earlier estimates of longevity previously reported by Osmundson et al. (1997). Catch rates of sympatric species also provide clues to shifts in fish community structure. Although not statistically significant, the apparent decrease in roundtail chub catch rates over the last 10 years suggests the need for future monitoring of this native species. Netting results also documented a significant rise in two species of potentially problematic non-native fish, white sucker and black bullhead.

The exercise in predicting change in adult numbers had mixed results. When predictions were made for past years for which population estimates in the following year were available for comparison, some predictions matched the population estimates fairly closely while others were substantially different. The population point estimates, against which we gauge our predictions, may be too imprecise. Alternatively, the length-frequency histograms may not provide an accurate enough portrayal of the true proportion of fish about to recruit. In either case, the method appears to be unreliable in predicting recruitment.

For recruitment, growth, and dispersal studies, it is important that these intensive capture surveys occur in consecutive years, rather than every other year or once every three years. The current regime of three consecutive years of study followed by resting the population for three consecutive years allows a good balance between the need to adequately monitor the population and learn other important life-history information and the need to minimize both handling stress on the fish and the disruption of the fishes' backwater refuges.

The Colorado River population of Colorado pikeminnow has made progress toward recovery during the last 10 years. Because it is a long-lived fish with a long generation time, the recovery process is a slow one. At the end of the 1980s, future prospects for this population appeared bleak. However, during the 1990s, those prospects improved. In addition, a recently built fish ladder has connected the Colorado River population with a small remnant population in the Gunnison River, estimated at 11-13 individuals (Burdick 2001).

McAda and Ryel (1999) demonstrated a link between year-class strength of Colorado pikeminnow in the Colorado River and the hydrological regime. Fortuitous events in the mid-1980s appear to have been responsible for setting the conditions that resulted in strong Colorado pikeminnow year-classes, i.e., two years of large floods followed by two years of moderately high spring runoff flows. To continue the recovery process, managers need to be mindful of this crucial flow-reproduction link. If these improved reproduction and recruitment rates, begun in the mid-1980s and early 1990s, can be perpetuated by the restoration of critical flow regimes, additional management actions will be needed to increase the availability and quality of adult habitat. Availability of sufficient adult habitat will be crucial in ensuring long-term viability of this population. A management strategy that emphasizes riverine ecosystem restoration will have the most chance of successfully leading to full recovery of Colorado pikeminnow in the Colorado-Gunnison basin.

CONCLUSIONS

1) Abundance of Colorado pikeminnow in the upper Colorado River increased during the 1980s and during the 1990s.

2) Use of closed-model, capture-recapture, population estimation appears to be the best single method for tracking Colorado pikeminnow abundance through time, but population dynamics are best interpreted when all sources of information and lines of evidence are utilized. These include not only population estimates, but also changes in netting catch rate, electrofishing catch rate, mean body condition and dispersal patterns.

3) The population of Colorado pikeminnow in the Colorado River has a male:female sex ratio of 1:1.

4) Females are not only larger than males on average but they can also attain larger sizes than males.

5) Difference in size between males and females is due to differences in growth rate and apparently not due to differences in mortality rates.

6) Female Colorado pikeminnow are estimated to attain 900 mm long in an average of 39 years.

7) During 1992-2000, densities (as reflected by catch rates) of two potentially problematic non-native fish species, white sucker and black bullhead, significantly increased in the Colorado River.

RECOMMENDATIONS

- Continue monitoring via periodic capture-recapture population estimates.

- Field efforts should occur in three consecutive years to maximize growth and dispersal information and also to allow averaging of annual estimates for blocks of years if annual estimates prove too imprecise to discern year-to-year trends as was the case here. This averaging may not be necessary if additional annual effort results in greater precision.

However, it is best to continue with three-year, back-to-back sampling blocks so that averaging can still be done if better precision does not materialize as planned.

- Three years of rest should separate the ending of one field effort and the beginning of the next to allow extended blocks of time in which the population can carry out its life functions with minimal disruption to behavioral and physiological processes. Thus, the end point of each three-year field effort would be six years apart.

- Confidence intervals around the point estimates need to be reduced, particularly for the lower-reach estimates so that a CV $\leq$ 20% is attained. Hence, I recommend that in years of sampling, effort should be increased from three passes to four passes in the upper reach and from two passes to four in the lower reach. This will likely require four two-person crews to work simultaneously five days per week for 6-8 weeks from mid-April to mid-June.

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APPENDIX

Appendix Table I. Number of total captures and recaptures (a subset of total captures) of Colorado pikeminnow of three length classes in each of two sampling passes in the lower reach study area, 1992-1994 and 1998-2000. Note: no data for 1991 appear here because only one sampling pass was made in the lower reach that year.

Size class (mm TL)	Total pass 1	Total pass 2	Pass 2 recaptures marked in pass 1
		1992	
≥ 250	18	15	1
≥ 450	4	9	1
≥ 500	2	5	1
		1993	
≥ 250	51	41	4
≥ 450	44	35	4
≥ 500	26	13	2
		1994	
≥ 250	47	25	4
≥ 450	37	14	1
≥ 500	30	10	1
		1998	
≥ 250	31	61	6
≥ 450	16	28	2
≥ 500	11	18	1
		1999	
≥ 250	38	24	2
≥ 450	25	7	0
≥ 500	13	4	0
		2000	
≥ 250	35	19	1
≥ 450	32	15	1
≥ 500	24	11	1

Appendix Table II. Number of total captures and recaptures (a subset of total captures) of Colorado pikeminnow of three length classes in each of three sampling passes in the upper reach study area, 1991-1994 and 1998-2000.

Size class (mm TL)	Total pass 1	Total pass 2	Pass 2 recaptures marked in pass 1	Total pass 3	Pass 3 recaptures marked in pass 1	Pass 3 recaptures marked in pass 2
1991						
≥ 250	23	17	4	25	2	0
≥ 450	22	16	4	24	2	0
≥ 500	20	15	4	21	1	0
1992						
≥ 250	21	25	2	23	1	1
≥ 450	21	24	2	22	1	1
≥ 500	21	23	2	19	1	1
1993						
≥ 250	31	31	6	33	5	6
≥ 450	30	30	6	32	5	6
≥ 500	27	23	5	27	5	4
1994						
≥ 250	27	37	3	38	2	4
≥ 450	27	37	3	38	2	4
≥ 500	20	34	2	32	1	4
1998						
≥ 250	46	73	8	52	4	9
≥ 450	46	70	8	51	4	9
≥ 500	46	70	8	46	4	9
1999						
≥ 250	52	65	8	55	3	15
≥ 450	52	62	8	54	3	15
≥ 500	50	58	8	49	3	14
2000						
≥ 250	52	51	8	29	2	2
≥ 450	51	51	8	29	2	2
≥ 500	48	50	8	27	2	2

Appendix Table III. Population point estimates ($\hat{N}$), standard errors (SE), probability of capture ($\hat{p}$) and coefficient of variation (CV) from Colorado pikeminnow sampling in the upper and lower reaches of the Colorado River study area, 1991-1994 and 1998-2000.

		Upper reach				Lower reach				
Year	Length (mm)	$\hat{N}$	SE	$\hat{p}$	CV	$\hat{N}$	SE	$\hat{p}$		CV
1991	> 250	215	75.599	0.0991	35.2	--	--	--	--	--
1991	> 450	202	70.447	0.1025	34.9	--	--	--	--	--
1991	> 500	197	76.332	0.0946	38.7	--	--	--	--	--
1992	> 250	381	173.149	0.0605	45.4	151	95.100	0.12	0.10	63.0
1992	> 450	358	162.671	0.0623	45.4	24	12.247	0.17	0.38	51.0
1992	> 500	316	142.320	0.0665	45.0	8	3.000	0.25	0.62	37.5
1993	> 250	163	29.474	0.1940	18.1	435	174.310	0.12	0.09	40.1
1993	> 450	153	27.233	0.2010	17.8	323	126.769	0.14	0.11	39.2
1993	> 500	130	25.584	0.1980	19.7	125	60.795	0.21	0.10	48.6
1994	> 250	368	107.134	0.0923	29.1	249	94.950	0.19	0.10	38.3
1994	> 450	368	107.134	0.0923	29.1	284	182.606	0.13	0.05	64.3
1994	> 500	337	111.990	0.0852	33.2	170	105.476	0.18	0.06	62.0
1998	> 250	441	79.576	0.1294	18.0	282	89.182	0.11	0.22	31.6
1998	> 450	420	75.418	0.1327	18.0	163	81.525	0.10	0.17	50.0
1998	> 500	394	70.368	0.1370	17.9	113	69.606	0.10	0.16	61.6
1999	> 250	356	55.054	0.1610	15.5	324	169.115	0.12	0.07	52.2
1999	> 450	339	52.078	0.1651	15.4	--	--	--	--	--
1999	> 500	307	47.699	0.1703	15.5	--	--	--	--	--
2000	> 250	463	116.406	0.0950	25.1	359	234.691	0.10	0.05	65.4
2000	> 450	456	114.632	0.0956	25.1	263	169.245	0.12	0.06	64.4
2000	> 500	415	103.360	0.1005	24.9	149	92.871	0.16	0.07	62.3