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STUDIES OF COLORADO SQUAWFISH IN THE UPPER COLORADO RIVER



Final Reports

Recovery Implementation Program

Project No. 14

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STUDIES OF COLORADO SQUAWFISH IN THE UPPER COLORADO RIVER

REPORT A

GROWTH AND SURVIVAL OF COLORADO SQUAWFISH IN THE UPPER COLORADO RIVER

D. B. Osmundson, R J. Ryel and T. E. Mourning
1996

REPORT B

NON-SPAWNING MOVEMENTS OF SUBADULT AND ADULT COLORADO SQUAWFISH IN THE UPPER COLORADO RIVER

D. B. Osmundson, M. E. Tucker, B. D. Burdick, W. R. Elmblad and T. E. Chart
1997

REPORT C

STATUS AND TRENDS OF THE COLORADO SQUAWFISH IN THE UPPER COLORADO RIVER

D. B. Osmundson and K. P. Burnham
1996

FINAL REPORTS
FOR RECOVERY IMPLEMENTATION PROGRAM
PROJECT NO. 14

U.S. FISH AND WILDLIFE SERVICE
COLORADO RIVER FISHERY PROJECT

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Cover:

Ptychocheilus lucius; photograph by Douglas B. Osmundson ©

SYNOPSIS

Introduction

This volume binds together three separate reports on life history and population studies of the Colorado squawfish (*Ptychocheilus lucius*) in the upper Colorado River. Principal topics covered are, 1) growth and adult survival rates, 2) dispersal patterns of sub- and young adults, and 3) status and trends of the Colorado River population. One integrated study design and field effort was used to collect most of the data used in these investigations. At the beginning of each report an executive summary provides the highlights of that study. The following is a synopsis of the collective results along with recommendations for future studies and management activities.

Growth rate, survival rate, and dispersal patterns are fundamental components of most demographic studies of long-lived species and are essential to understanding population dynamics. Determination of population status and trend and identification of factors limiting population increase are requisite to formulating recovery goals and management strategies for endangered species.

Colorado squawfish, an endangered, long-lived, cyprinid endemic to the Colorado River system, has been the focus of much life-history research in recent years. However, many fundamental questions regarding its life history remain unanswered. *Ptychocheilus lucius* is well known for its potential to grow to large size and for its annual, potamodromous, spawning migrations. However, previous studies of age and growth of Colorado squawfish have relied on scale analysis. Because of the inherent problems in scale-based aging and growth estimation for long-lived species, there was a need to refine and validate existing growth estimates. Though spawning migrations and the long-distance drift of resulting larvae have been well documented, little is known about dispersal patterns of juveniles and young adults. In addition, no serious attempt has been made to estimate population size in any of the extant riverine populations. For the Colorado River population, no previous effort had been made to assess recruitment or adult survival rates.

Much can be learned of long-lived fish from mark-recapture studies. Such studies require multi-year, intensive capture efforts that are systematic and river wide in scope. Most importantly, a large number of fish representing a significant portion of the population must be sampled and a safe, reliable method must be used to individually and permanently mark the fish. For this study, two relatively new methods greatly facilitated the investigators to meet these requirements: 1) an effective netting technique that trapped Colorado squawfish in backwaters where they are seasonally concentrated, and 2) passive integrated transponder (PIT) tags that are small, implanted internally, and read externally with an electronic scanner.

Methods

For these studies backwaters were trammel netted during spring runoff each year from 1991 through 1994. Subadults and adults congregate in these low-velocity habitats during runoff when main-channel flows increase dramatically. Fish were entrapped in backwaters by a method dubbed 'scare and snare'. Using a jon boat and a crew of two people, the open end of each backwater was first blocked with a trammel net; the boat then entered the backwater by passing over the net with the motor raised. Once inside, the boat was used to scare fish toward the net by vigorously motoring back and forth beginning at the far end of the backwater and working towards the mouth. Nets were pulled as soon as sufficient 'scare' effort was expended (5-15 min depending on backwater size). The entire range of the Colorado River population upstream of the Green River confluence was systematically sampled each year, with three complete sampling passes made annually through the upper reach (upstream of Westwater Canyon) and two annual sampling passes made through the lower reach (downstream of Westwater Canyon). With each pass, every backwater suspected of harboring adult Colorado squawfish was netted. Sampling effort was augmented with electrofishing in some segments where backwaters were few. Additional capture data from concurrent studies were utilized to the extent possible. Data from fish recaptured during other studies in 1995 were also used to supplement growth and movement data.

Results and Discussion

Growth, age and survival

Mean annual growth rates of 3- to-6-year-old fish were calculated from measured lengths of individuals aged by scale analysis. The highest rate was 82.0 mm/year when fish were three years old. By the time fish were six years old, average growth rate declined to 32.2 mm/year. Growth rates for older fish were estimated from changes in total length (TL) of marked and later recaptured individuals. These annual growth increments were averaged for fish within 50 mm size groups. For fish 500-549 mm TL, annual growth increments averaged 22.2 mm/yr. For fish ≥ 550 mm TL, growth increments averaged 8.7 mm/year, but varied (although not significantly) from 15.0 (700-799 mm-long fish) to 3.9 mm/year (800-899 mm-long fish). Thus, rate of growth slows markedly after about age 10, although there appears to be an increase in rate when fish are between 650 and 800 mm TL; beyond 800 mm TL, growth apparently slows again. For fish up to 10 years old, results here were similar to those reported in previous studies. However, measured increments from capture-recapture data indicated that previous scale-based methods over estimated real growth rates in older fish (> 10 years old).

Based on these new growth curves, ages of fish of various length were calculated. Simulations indicated broad ranges of ages for fish of given lengths, especially fish ≥ 550 mm TL: it takes 10-22 ($\overline{X}$ = 15) years for 95% of the fish to reach 600 mm in length; 16-30 ($\overline{X}$ = 25) years to reach 700 mm; 20-40 ($\overline{X}$ = 32) years to reach 800 mm.

Annual survival rates for fish ≥ 550 mm TL were estimated by comparing measured size distributions with simulated stable age and size distributions; these estimates ranged from 0.83-0.88 ($p < 0.05$) with the best fit at 0.86. This estimate was later corroborated with results from the Cormack-Jolly-Seber model which utilized capture-recapture histories of individual fish. An annual survival rate of approximately 0.86 is not considered low for a long-lived fish; therefore, low adult survival rate is likely not a major cause of the decline of this population. However, survival rate does affect the potential for population increase; hence, any management activity that can increase this rate would likely benefit this population.

Distribution and dispersal patterns

Longitudinal distribution of Colorado squawfish was described in terms of mean size of fish and mean number of adults captured per net in six river strata. Average length of Colorado squawfish progressively increased upstream and was most pronounced during the first years of the study. During 1991-1992, most adults (> 500 mm TL) were concentrated in the upper reach and very few adults were found in the lower reach. As the study progressed, demographics changed as 2-3 consecutive strong year classes, hatched during the mid-1980's, grew and dispersed as they recruited to the adult population. As a result, average length increased in lower-reach strata and decreased in upper-reach strata. By 1993, there was a five-fold increase in catch rates of adults in the lower reach.

Subadult and adult Colorado squawfish were often patchily distributed during the spring sampling period. The proportion of sampled backwaters yielding Colorado squawfish ranged from 16 to 50% depending on the year and river strata sampled (the river was subdivided into 6 study strata based on changes in average channel gradient: three below Westwater Canyon, strata 1-3, and three above Westwater Canyon, strata 5-7; Westwater Canyon itself, Stratum 4, was not sampled). Within Stratum 1 (most downstream stratum) as much as 55% of the total fish captured within a given year came from a single backwater; within Stratum 3, as much as 89% came from a single backwater; within Stratum 6, as much as 78%; within Stratum 7, 52%. The highest densities of backwaters occurred in the Grand Valley portion of the river: 0.78-0.91 backwaters/km in Stratum 6 (18-mile reach) and 0.62-0.75 backwaters/km in Stratum 7 (15-mile reach).

Movements of fish captured one year and recaptured in a subsequent year were compared among size classes of fish and between those fish initially captured in the lower reach and those captured in the upper reach. Of those Colorado squawfish initially captured and tagged in the upper reach, only 16% were later located > 10 km from the previous capture site; of those tagged in the lower reach, 58% were later located > 10 km from the previous site. Of those movements > 10 km, 80% were directed upstream for upper-reach-tagged fish; 68% were directed upstream for lower-reach-tagged fish. Also, for lower-reach-tagged fish, 44% of movements > 10 km were movements from the lower reach to the upper reach, whereas none of the fish located in the upper reach during the study period were later recaptured in the lower reach. Distance moved was inversely related to fish size: displacement of fish < 550 mm TL averaged 33.6 km; for those > 550 mm TL, average displacement was only 7.5 km.

The smallest documented fish that moved from the lower to the upper reach was no longer than 449 mm when it made its move.

Movement of young adult Colorado squawfish was likely a response to their changing food requirements as they grew and matured. A net shift in abundance to upstream reaches was probably because upstream movements were rewarded with greater food availability. Two lines of evidence supported this hypothesis: 1) catch rates of roundtail chub (*Gila robusta*) and bluehead (*Catostomus discobolus*) and flannelmouth sucker (*C. latipinnis*), likely prey of adult Colorado squawfish, were significantly higher in the upper reach than in the lower reach, and 2) body condition of Colorado squawfish decreased with fish size in the lower reach but increased with fish size in the upper reach. Results suggested that young Colorado squawfish move more than older ones and that upon arrival to the upper reach they move less. Evidently, older fish establish home feeding ranges in areas they have found to be most productive and have little need for further exploratory movements. The reach upstream of Westwater Canyon evidently provides the best adult feeding opportunities in the upper Colorado River.

Population status and trends

To determine status, we estimated the size of the subadult and adult population. To determine short term trends, we examined the extent and frequency of reproduction and recruitment by monitoring larval and young-of-the-year catch rates and looked for significant changes in age or size structure of the population over the past 20 years. Past long-term trends could not be quantified because of a lack of historical data.

Population abundance was estimated with both open- and closed-population models using capture-recapture data. Size frequency analysis from lengths of captured fish was used to assess trends in age structure of the population both among reaches and among time periods. Upper-reach, size-structure data were compared with those from earlier periods for which data sets were sufficiently large; these included 1974-1976, 1979 and 1982. Also, size frequency data from the lower reach, coupled with age information from scale analyses, was used to determine the frequency of strong year classes during recent times. Reproductive success in the upper reach over a nine-year period (1986-1994) was evaluated by systematically sampling for Colorado squawfish larvae with hand seines and young-of-the-year (YOY) with beach seines each summer and fall, respectively. Summary data from the Interagency Standardized Monitoring Program was also examined to compare upper reach data with lower reach YOY capture rates.

Size of the adult subpopulation in the upper reach, averaged over the four-year study period, was estimated to be 263 individuals (95% C. I. = 161-440) using program CAPTURE and 253 (95% C. I. = 186-333) using program RECAP, or an average of 4.0-4.2 fish per mile of river. In the lower reach, estimated size of the subpopulation (adults and subadults), averaged over a three-year period, was 344 individuals (95% C. I. = 196-604) using program CAPTURE and 385 (95% C. I. = 202-733) using program RECAP, or an average of 3.1-3.4

fish per mile. For the river as a whole (Palisade, Colorado to the Green River confluence, Utah), size of the subadult and adult population was estimated at around 600-650 during the period of study.

A relatively large number of subadults (300-400 mm TL) were found in the lower reach during 1991. Scale analyses indicated these fish were from three year-classes, hatched in 1985, 1986, and 1987. By 1992, these fish were distributed throughout the river system. Trammel-netting catch-per-unit effort in the upper reach steadily increased over the four years of study. Though catch rates of larger adults (> 550 mm long) did not significantly increase, catch rates of subadults and young adults (< 550 mm long) increased five-fold. Size-frequency analysis of lower-reach fish indicated the 1985-1987 cohorts were the strongest year classes produced since at least 1977, and no similarly strong year classes have been produced since 1987. Catch rates of larvae and YOY in the Grand Valley also indicated that reproductive success in 1986 and perhaps in 1987 was relatively high, and all other years through 1994 had comparatively low catch rates.

Until this recent pulse of young adults was produced, the vast majority of adults were found in the upper reach; the lower reach contained almost exclusively individuals < 500 mm long. Thus, in recent years, the bulk of the adult population was contained in the upper reach. There, very few individuals < 450 mm long are found, indicating that recruitment to the upper reach subpopulation occurs almost entirely from colonization of young adults migrating there from the lower reach. In contrast, size frequencies recorded during the mid 1970's indicate that significant recruitment in the upper reach may formerly have occurred via young rearing within the upper reach.

Though some level of recruitment appears to occur every year, the Colorado River population of Colorado squawfish is probably sustained by strong year classes that occur very infrequently. Though adult survival rate is likely fairly constant from one year to the next, recruitment is highly variable. Long-term, average, annual rates of recruitment are unknown and therefore it is difficult to discern whether recruitment balances mortality over the long term. Given the current low population size in comparison with historical accounts that suggest the species was formerly abundant, it is likely that recruitment has not kept pace with mortality. However, this population appears quite capable of recovering on its own if the frequency of strong year classes can be increased. This will require the improvement of environmental conditions that currently limit reproductive success and survival of young.

CONCLUSIONS

1) Growth rate in Colorado squawfish older than 10 years is slower than previously thought.

2) Annual increases in length average 82 mm per year in 3-year-olds but decline to 4 mm per year in fish > 800 mm long.

3) Size at which most individuals reach sexual maturity (428-503 mm TL; Seethaler 1978) is attained at about seven years of age.

4) Size of fish of a given age is highly variable: simulations indicated lengths of 10-year-olds may vary by 100 mm; of 20-year-olds, 200 mm.

5) Longevity is likely greater than previously thought; simulations indicated that most individuals 800 mm long are estimated to be between 20 and 40 years old; those 900 mm long are estimated to be at least 32 years old and perhaps considerably older.

6) Annual adult survival rate is not particularly low; two separate estimators produced consistent results: 0.86.

7) Historic growth and survival rates are unknown.

8) Average size of Colorado squawfish in the Colorado River increases in an upstream direction; over time adults become concentrated in the upper reach.

9) Though subadults and adults are found in backwaters throughout the river during spring runoff, some backwaters have consistently higher catch rates than others.

10) Small adults move greater distances over time than do larger adults, and fish in the lower reach (mostly small adults) move greater distances between captures than do fish in the upper reach.

11) There is considerable movement of adults from the lower to the upper reach but little to no movement from the upper to lower reach.

12) Body condition of subadults is high during spring in the lower reach but declines as they grow to adult size; conversely, in the upper reach, condition increases as adults grow.

13) Net displacement of adults to the upper reach and improved body condition is likely related to significantly higher densities of native forage fish there.

14) Colorado squawfish use long-distance dispersal to best meet their life-stage specific needs: larvae disperse downstream to warm nursery reaches where they remain and grow until reaching adult size; adults disperse upstream to reaches rich in native forage fish.

15) Population abundance in the Colorado River is relatively low: a total of 600-650 adults and subadults was estimated for the period of study.

16) Compared to historical accounts, population abundance today appears low and suggests the long-term trend of this population has been downward.

17) Maintenance of the population appears to depend on occasional strong year classes.

18) Two to three consecutive, strong cohorts of Colorado squawfish were produced during the mid-1980's and recruited to the adult population in the early 1990's.

19) Frequency of strong year classes has been very low over the past 20 years.

20) Because of low and fluctuating adult numbers due to the infrequency of strong year classes, the population appears vulnerable to extinction.

21) This population has the capacity to increase in abundance on its own without augmentation if focused management activities are formulated, implemented, and successful at boosting recruitment rates, perhaps through increasing the frequency of strong year classes.

22) Prospects for the continued persistence and increased abundance of this population likely will depend on identification of factors that limit spawning and hatching success and survival of young, and most importantly, the effectiveness of recovery actions aimed at addressing such factors.

RECOMMENDATIONS

1) Intensive, multi-year, scare-and-snare, mark-recapture efforts should be made periodically to adequately monitor the status and trend of this and other upper basin populations. A three-year effort period followed by a three-year non-effort period would provide an abundance estimate every five years. Because the last effort for this population ended in 1994, the next three-year effort period should begin in 1998.

2) Some benefit to this population could be achieved by boosting the annual adult survival rate. An increase from the current 0.86 to 0.90 would result in a doubling of the population in 18 years. Four sources of mortality that might be reduced through management activities include:

   a) Stranding of adults in gravel pit ponds after spring runoff. Gravel pits located in the floodplain should be made to drain with descending flow or sufficiently diked to exclude flood waters and squawfish.
   b) Angler-related mortality. Increase law enforcement and information and education programs, especially in the Grand Valley.
   c) Choking mortality from ingestion of channel catfish. Reduce numbers of riverine channel catfish by whatever means feasible.
   d) Biological sampling mortality. Use only approved electrofishing equipment and procedures. Limit time trammel nets are set to 15 minutes. Train biologists in proper handling and holding procedures, and implantation techniques for radio-tags and PIT tags.

3) Conduct research to identify the relationship between environmental variables and annual reproductive success and survival of young in the Colorado River. Results from such studies would provide the guidance needed for implementing effective management activities that could boost recruitment rates.

4) Boost the recruitment rate by implementing appropriate management activities. If the average annual recruitment rate was doubled, the population could double in size in 5-6 years; in 18 years it could be 10 times the size it is today. This assumes the long-term recruitment rate now balances the mortality rate, i.e., 14 % and recruitment is doubled to 28% while maintaining the current mortality rate. Average annual recruitment rate could be doubled by increasing the frequency of strong cohorts from once every 10 years to once every five years. Such population increase would necessitate the availability of adequate adult habitat.

5) Conduct bioenergetics studies to estimate how many adults the river can presently support and could potentially support with the implementation of appropriate management activities. Such estimates would provide the basis for recovery goals.

GROWTH AND SURVIVAL OF COLORADO SQUAWFISH IN THE UPPER COLORADO RIVER

FINAL REPORT

MAY 1996

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EXECUTIVE SUMMARY

Growth and survival rates are fundamental components of most demographic studies of long-lived species and are essential to understanding population dynamics. Determination of population status and trend and identification of factors limiting population increase are requisite to formulating recovery goals and management strategies for endangered species. The primary objective of this study was to refine previous estimates of Colorado squawfish growth rate in the Colorado River by minimizing the use of scale analyses, a technique deemed unreliable for estimating growth in older fish. A secondary objective was to estimate adult survival rate for this population. A third objective was to estimate age of Colorado squawfish of various sizes and provide some estimate of potential longevity.

Growth and adult survival rates of Colorado squawfish (*Ptychocheilus lucius*) in the upper Colorado River were estimated using fish captured from 1990 through 1995. Mean annual growth rates of 3- to-6-year-old fish were estimated from measured lengths of individuals aged by scale analysis, and ranged from 32.2 (6-year-olds) to 82.0 (3-year-olds) mm/year with coefficient of variation near 1.0. Growth rates for older fish were estimated from changes in total length (TL) of marked and later recaptured individuals. These annual growth increments were averaged for fish within 50 mm size groups. Rates were highest for fish 400-449 mm TL with length increases averaging 42.7 mm/year, and declined to 22.2 mm/year for fish 500-549 mm TL. For fish ≥ 550 mm TL, growth increments averaged 8.7 mm/year, but varied (although not significantly) from 3.9 to 15.0 mm/year depending on the size group. Length frequencies by age for 8-year-old and older fish were estimated by simulating growth beginning with the distribution of lengths for 7-year-old fish and adding annual growth increments. A simulated population of 10,000 fish was used with growth increments randomly selected from the measured distributions of growth increments within 50-mm size classes to provide an estimate of range in length at each age for 95 % of the population. Lengths of individuals varied by 100 mm for 10-year-old fish and by as much as 200 mm for fish 20 or more years old. The range of ages for a given length was also highly variable with ages differing by up to 20 years for fish > 800 mm TL. Survival rates for fish ≥ 550 mm TL were estimated by comparing measured size distributions with simulated stable age and size distributions; these ranged from 0.83-0.88 ($P < 0.05$) with the best fit at 0.86.

Also, in the Discussion, we offer an explanation on the current absence of very large fish often reported in historical accounts and discuss additional mortality factors arising during the past 75-100 years that might have lowered adult survival rates. Of these, choking on the spines of ingested channel catfish (*Ictaluras punctatus*), an introduced species, may be the most serious. Though lack of historical data on growth and survival rates precludes comparisons with past rates, estimates provided here can serve as a baseline for future population monitoring efforts.

INTRODUCTION

Growth and survival rates are fundamental components of most demographic studies of long-lived species and are essential to understanding population dynamics. Determination of population status and trend and identification of factors limiting population increase are requisite to formulating recovery goals and management strategies for endangered species. Colorado squawfish (*Ptychocheilus lucius*), an endangered, long-lived, cyprinid endemic to the Colorado River system, has been the focus of much life-history research in recent years. Previous studies of age and growth of Colorado squawfish have relied on scale analysis, whereby age is determined by counting numbers of scale annuli and growth is estimated as the difference in calculated fish lengths predicted from relationships between length and radius of scale annuli (e.g., Vanicek and Kramer 1969, Seethaler 1978, Musker 1981, and Hawkins 1992). Problems inherent in scale-based aging and growth estimation for long-lived species prompted us to refine existing growth estimates of Colorado squawfish by utilizing newly available, mark-recapture-based, growth data. Age estimates derived from the refined growth estimates enabled us to also assess adult survival rates.

Techniques used in scale analyses are fairly standardized (e.g., Tesch 1968, Carlander 1969). While results of such analyses have proven reliable for some species, for others they have been largely unreliable (Beamish and McFarlane 1987). Scales were considered by Scoppetone (1988) to be unreliable for accurately aging many western North American catostomids and cyprinids because age was considerably underestimated in long-lived individuals. Although validation of aging techniques using known-age fish is a critical component of studies attempting to estimate age and growth from scales, such validation is often lacking in non-game fish due to the scarcity of known-age individuals. Aging other bony structures (e.g., vertebrae, otiliths, opercles, etc.) may corroborate results from scales but this constitutes only a partial validation at best (Beamish and McFarlane 1983), and requires sacrifice of the animal.

Problems specific to aging Colorado squawfish include the lack of annulus formation during the first year, and the compression and loss of outer annuli by older fish (Hawkins 1992). Lack of first-year annulus formation has been corrected by adding a year to the number of annuli (Seethaler 1978, Hawkins 1992), but problems with distinguishing and counting outer annuli can result in underestimation of ages and population age frequencies, resulting in many fish assigned to the age where the method fails (Beamish and McFarlane 1983, Hawkins 1992). Hawkins (1992) suggested that differences in average annual growth increments for Colorado squawfish > 500 mm TL, calculated from scales (30 mm/year) and those from recaptures of tagged fish (10-15 mm/year), may be due to a negative effect from Carlin dangler tags on tagged fish. Indeed, Floy tags, another type of external tag, reduce growth in trout (Carline and Brynildson 1972, Mourning et al. 1994), though not in largemouth bass (Tranquilli and Childers 1982).

The recently developed, small and internally-implanted Passive Integrated Transponder (PIT) tag enhances the ability to permanently mark individual fish and track growth through successive years. Burdick and Hamman (1993) reported 98-100 % tag verification 20-24

months after Colorado squawfish were experimentally implanted, and no difference in growth was detected between PIT-tagged fish and non-PIT-tagged controls. Use of PIT tags for marking fish should greatly reduce or eliminate any biases in growth assessment that were previously ascribed to Carlin dangler tags.

The primary objective of this study was to refine previous estimates of Colorado squawfish growth rate in the Colorado River by minimizing the use of scale analyses and instead relying on recaptures of PIT-tagged individuals. A secondary objective was to estimate adult survival rate for this population. The approach used to estimate survival was modified from models that estimate survival (e.g., Seber 1982) using declining numbers of increasingly older individuals in the population. A third objective was to estimate age of Colorado squawfish of various sizes and provide some estimate of potential longevity. In addition to addressing these objectives, we also discuss related topics including the disappearance of very large individuals reported in historical accounts and mortality factors that may have reduced survival rates in recent times.

METHODS

Extent of Study Area

The study area included the entire occupied range (≈ 300 km of river) of the Colorado squawfish in the upper Colorado River, upstream of the Green River confluence (Fig. 1). River locations described herein are in river kilometers (RK) from the Green River confluence (RK 0.0) and are conversions of river miles mapped by Belknap and Belknap (1974). Further upstream movement of this species is seasonally blocked by a diversion dam at RK 298.1 and is blocked all year by another diversion dam at RK 303.0. Upstream access in the Gunnison River, a major tributary entering the Colorado River at RK 275.1, is blocked all year by a diversion dam 3.5 km upstream of the mouth. Most adult Colorado squawfish live in the upper portion of the study area while earlier life stages are generally found in the lower portion (Valdez et al. 1982). The study area was divided into upper and lower reaches based on this general distribution of life stages, with Westwater Canyon (RK 181-200) the demarcation zone (Fig. 1). Westwater Canyon was not sampled for logistic reasons and because past studies have indicated that few Colorado squawfish are found there.

Fish Capture and Marking

From 1991 through 1994, an intensive effort was made between late April and mid-June to capture Colorado squawfish throughout the study area. At this time, Colorado squawfish are primarily found in low-velocity, off-channel habitats when main channel flows dramatically increase from spring runoff (Osmundson and Kaeding 1989). Trammel nets were used to capture squawfish from these sites. We quickly blocked the mouth of each backwater with a

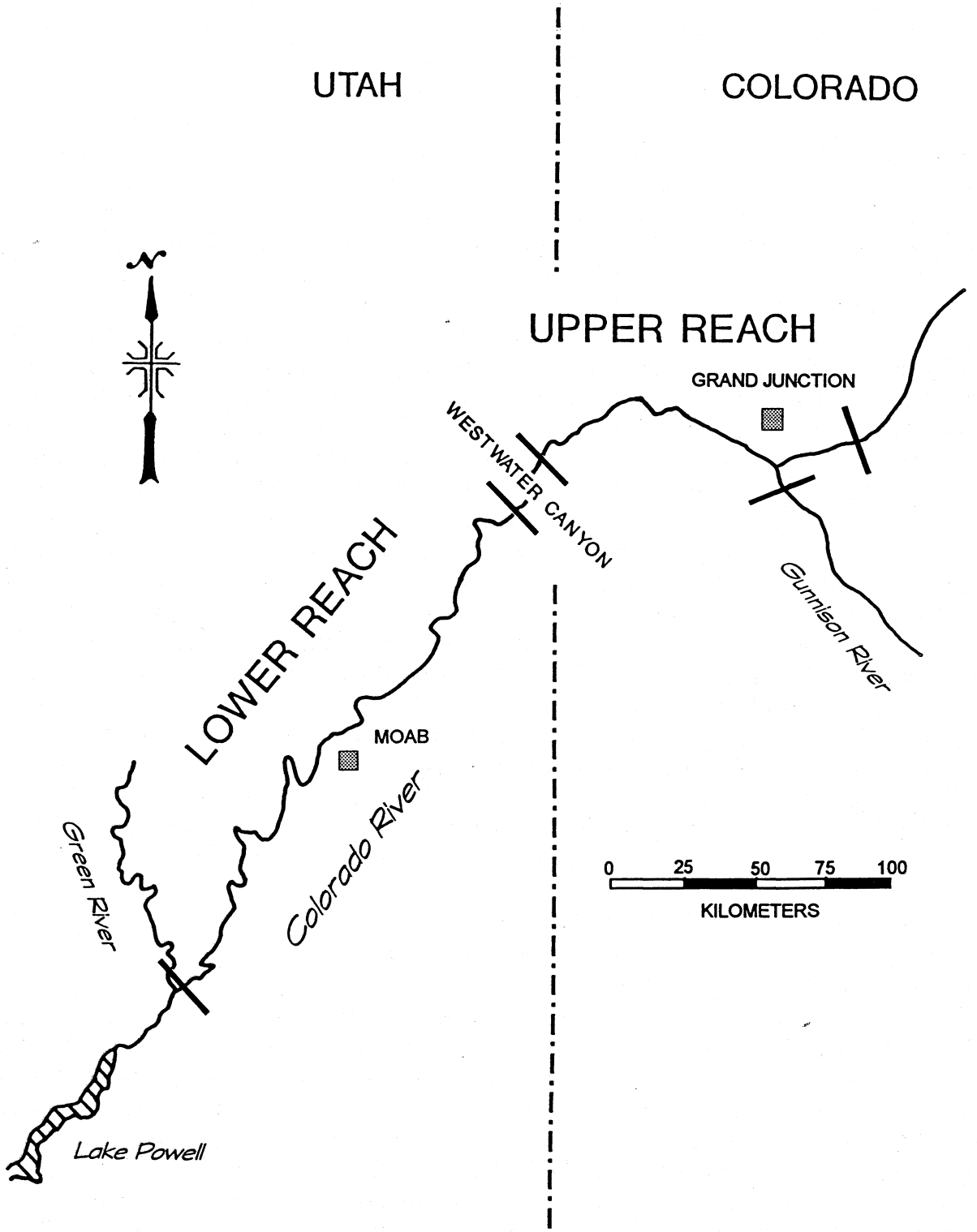


Figure 1. Map of the upper Colorado River study area.

net and used a motor boat to scare or 'drive' fish from inside the backwater toward the river channel, thereby ensnaring fish in the net (see Osmundson and Burnham, 1996 for more details). This procedure made netting an 'active' rather than a passive capture method. Three passes were made through the entire upper study area each spring. Two passes were made through the lower study area each spring. During each pass, we netted every backwater we suspected adult Colorado squawfish might use. In some portions of river, where backwater habitats were rare, both shorelines were electrofished with a 4.9-m, jon boat equipped with a Coffelt VVP-15 (Coffelt Manufacturing, Flagstaff, Arizona) using pulsed DC current.

Captured fish were scanned for a PIT tag, and tagged if one was not detected. PIT tags (Biomark, Inc., Boise, Idaho) were implanted in the body cavity using a hypodermic needle after fish were anesthetized with Tricane methanesulfonate. Each PIT tag had a unique, 10-digit, alpha-numeric code that was read with an electronic scanner and recorded in the field. PIT tags were inserted 2-5 mm posterior to the base of the left pelvic fin. Samples of five to eight scales were removed with forceps from between the lateral line and insertion of the dorsal fin. The scales were placed between wax paper and kept in labeled envelopes. Maximum total length (TL), as defined by Anderson and Gutreuter (1983), was measured and fish were released after recovery from the anesthetic.

We supplemented our data with additional capture records obtained from various sources, including those from a pilot netting and PIT-tagging exercise we conducted in the upper reach during 1990. The Colorado Division of Wildlife contributed 1991 through 1995 capture records and some recapture data was provided by the Utah Division of Wildlife Resources (UDWR); both agencies conduct annual electrofishing surveys of the river. U.S. Fish and Wildlife Service (FWS) capture records from a 1994-1996 survey of the lower 3.5 km of the Gunnison River (Burdick 1996), and from a 1995-1996 survey of flooded ponds near RK 262, were used. Length frequency data collected by FWS in 1982 were also utilized.

Calculation of Growth

The standard approach used in describing ages of fish is not intuitive. When the length of a fish at age 1 is reported, age 1 is not its first birthday (or hatchday) as one would expect but rather its first winter, i.e., the time when growth slows down or stops for the year and closely packed circuli are laid down. In the Northern Hemisphere, the convention is to standardize all birthdates as January 1 (Jearld 1983). A fish captured between its first and second winter period is described as being age 1+, implying that it is greater than one year old when in fact it may not have reached its first real birthday. Because we used measurements of fish rather than back-calculated estimates of length, we deviated from this convention and attempted to describe the length of Colorado squawfish at their approximate summer birth date.

We used a combination of techniques to determine mean length at various ages. Our goal was to utilize measured changes in length of individual fish as much as possible and minimize reliance on scale analysis. However, recaptures of juvenile and subadult Colorado squawfish were few so measurements of fish aged by various means, including scales (ages 2-7), were used for young fish.

Ages 0-7

Colorado squawfish average 7.7 mm long at hatching (Snyder 1981). For age 1 Colorado squawfish, mean length was determined using measurements of all fish seined on June 28, 1989 from backwaters near RK 87. A unimodal size distribution indicated these were all of one age group. For Colorado squawfish 2-7 years old, mean length at each age was derived from measurements of fish aged using scale analysis. These fish were captured between April 28 and June 21 (1991-1994) primarily from the lower reach and many were therefore 2-3 months younger than the reported age. Thus, beginning with 2-year-old fish, annual increases in length represent growth from one spring period to the next rather than from one hatching period to the next.

Scales were mounted wet on a microscope slide, a second slide was taped over it, and the scale allowed to dry inside. Scale images were magnified and projected for analysis using a Bausch and Lomb scale reader (Bausch and Lomb, Inc., Overland Park, Kansas). Scale annuli were counted and the missing first annulus (e.g., Seethaler 1978, Hawkins 1992) added to estimate age. Four to eight scales were examined from each fish and the number of annuli most frequently identified was used. We used scales from known-age, pond-reared Colorado squawfish (2-4 years old) for developing our technique and later testing our accuracy.

Ages 8 and older

For fish eight years old and older, sufficient recapture data were available for determining mean annual growth increments. Growth data were typically used from fish with capture-recapture intervals of 1 year. Thus, a growth increment for an individual fish was the difference in length at capture year i and year $i + 1$. However, because of low sample size for fish $\geq$ 600 mm TL, annual growth increments were also calculated for fish with recapture intervals of 2 or 3 years (total gain in length divided by the number of years between captures). Growth increments were averaged by size class of fish at initial capture year i. Size classes were in increments of 50 mm (e.g., 300-349, 350-399, etc.). Analysis of variance (ANOVA) was used to test for differences in growth rates among size classes.

Mean length at each age was first calculated by adding the appropriate mean increment of growth (based on length class) to the mean length of the preceding age. The average length of 7-year-old fish as determined from scale analysis was used as the starting point for these calculations. This process was continued until mean length reached 900 mm, roughly the upper size limit of Colorado squawfish captured from the Colorado River in recent years.

Monte Carlo simulation based on the mean and variance of the growth increments for each 50-mm size class was also used to estimate mean length at each age. Twenty simulations were conducted using different random number sequences. The mean and variance of 7-year-old fish, as determined using scales, was used to generate the initial size distribution. For a simulated population with 10,000 fish of each age, lengths for each age were calculated based upon the simulated distribution of sizes in the previous age class. From these simulations, the range of ages expected for a given length were also calculated.

To aid in constructing realistic growth simulations, statistical tests were conducted to determine if growth of fish in one year was related to growth in the following year, and whether differences occurred in mean growth among years. Using fish captured in multiple years, contingency table analysis was conducted to test the relationship in growth between years for individual fish. This analysis determined whether above (or below) average growth was related to above (or below) average growth in subsequent years. We used analysis of covariance (initial length as covariate) to test for differences in growth rates among years for the period 1991 through 1995.

Survival

Estimates

Survival rates were estimated for Colorado squawfish ≥ 550 mm TL. We assumed survival rates of juveniles and subadults were likely different from adult rates but had no way of assessing these rates. These estimates were limited to adults from the upper reach only (Fig. 1) because longitudinal variation in size distribution coupled with unequal sampling effort between lower and upper reaches would have biased whole-river length distributions. Estimates of adult rates were limited to fish ≥ 550 mm TL because Seethaler (1978) reported immature fish as large as 503 mm TL. Estimates were made using a modified Chapman-Robson (Seber 1982) approach where survival is based on declining numbers of individuals by age in the population. Because captured fish could not be reliably aged, estimates of survival were made by comparing length distributions from captured fish with theoretical length distributions. The method used makes the following assumptions, which are consistent with Ricker (1973):

1) survival rate is uniform with age over the range of ages examined;
2) survival rate is uniform over time, and does not vary among years;
3) recruitment to the first size examined is equal among years; and
4) sample is uniformly drawn from all ages/lengths considered, i.e., no effect of gear selectivity.

Theoretical length distributions (termed "stable length distributions") were calculated from age distributions assuming constant survival rates and constant recruitment into the youngest age class (termed "stable age distributions"), and age-length distributions generated in this

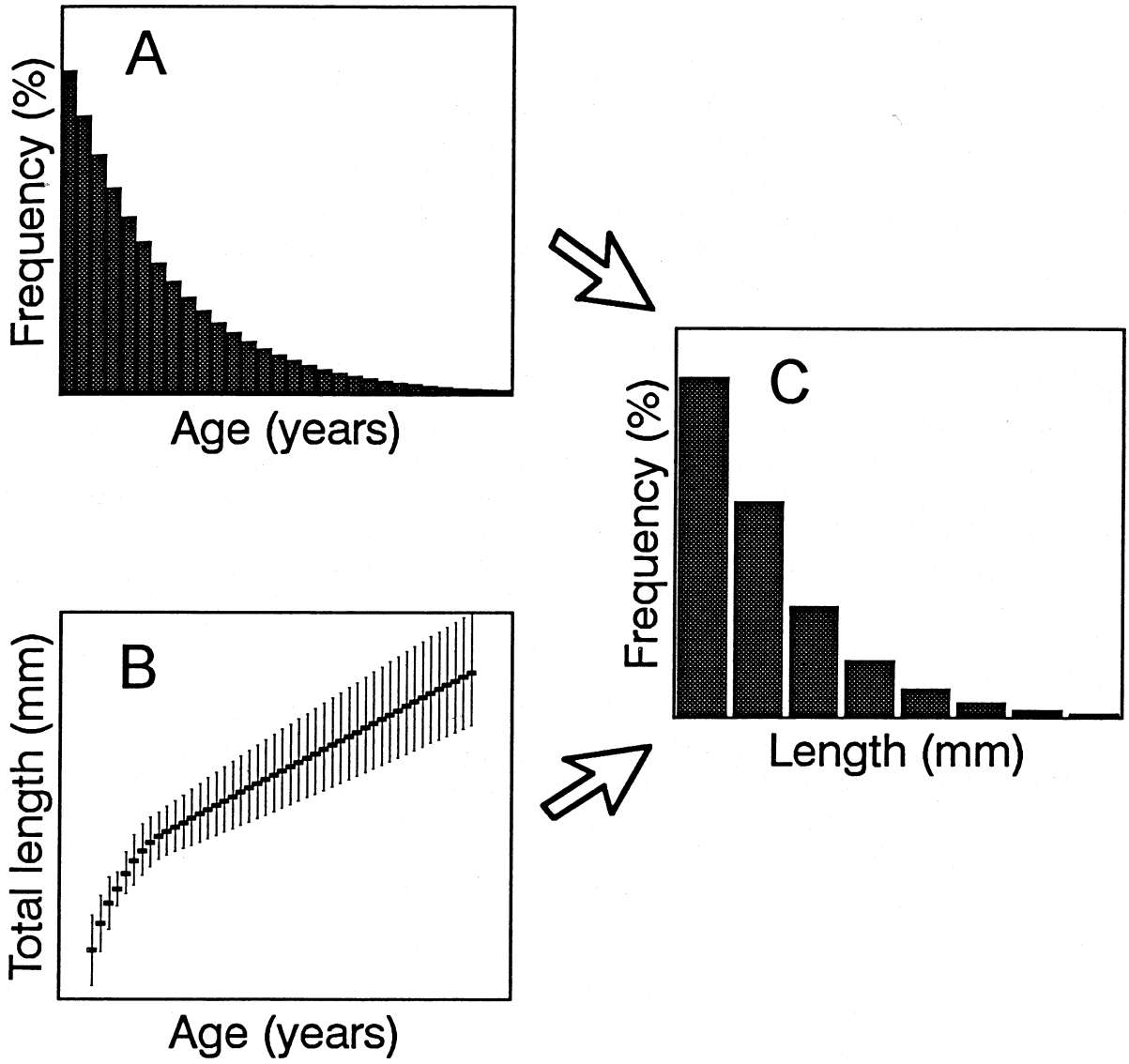


Figure 2. Calculation of stable length distribution (C) from stable age distribution (A) and age-length distribution (B). Stable age distribution (A) assumes a constant survival rate and constant rate of recruitment into the youngest age class. Age-length distributions are calculated from distributions of growth increments based on total length. Stable length distributions (C) were calculated using the relative number of fish for each length as determined by the age-length frequency distribution and the relative number of fish by age.

study (Fig. 2). The stable age distribution for constant survival rate *s* was calculated using:

$$N_i = N_{i-1} * s * (1-g)$$

where N_i is the relative number of fish of age *i* and g is the annual growth rate of the population. Simulations were conducted to select lengths for each age from the age-length distribution. Lengths were randomly selected from these distributions for 10,000 fish of each age, and the number of fish in 1-mm-TL increments was calculated by weighting the relative number in each age class. Survival rates for which the measured distributions did not differ significantly ($P > 0.05$) from the stable length distributions, using the Kolmogorov-Smirnov (KS) one-sample test, were considered to be "suitable" estimates.

Tests of Assumptions

Statistical tests were conducted to assess whether the observed population structure was consistent with the assumptions listed above. Comparisons between length distributions of fish captured in each year (1982, and 1991 through 1995) were made using the K-S two-sample test to assess the constancy of the age structure between years. Stability in the age structure would be consistent with relatively constant recruitment into the youngest age class, and constant survival among years and over ages and lengths. We compared distributions of fish captured with trammel nets with those captured with electrofishing (K-S two-sample test) to determine whether all capture data could be used. Also, we used annual, trammel-net catch rates of Colorado squawfish ≥ 550 mm TL as a measure to assess (ANOVA) whether population abundance was relatively stable (i.e., $g \approx 0$) during 1991 through 1994. Though effort among net sets was unequal, average effort of net sets was assumed equal among years.

RESULTS

Growth and Age

Growth of Colorado squawfish in the Colorado River is relatively rapid through about age 10 (Tables 1 and 2). At this age, Colorado squawfish average approximately 550 mm TL. Our estimates of mean lengths by age were similar to those reported by other researchers, but only through about age 10 (Fig. 3a). Our estimate of mean age for fish 600 mm TL was 15 years; for those 700 mm TL, 25 years; 800 mm TL, 32 years. Rate of growth slows after about age 10, although there may be a rate increase when fish are between 650 and 800 mm TL; beyond 800 mm TL, growth apparently slows again (Table 2). However, differences in mean annual growth increments among all size classes > 550 mm were not statistically significant. Growth rate differences among years (1991-1995) were not found for fish ≥ 345 mm TL (ANCOVA, df = 4, 71, F = 0.34, $P = 0.85$). Relationships between growth in one year and subsequent years was not found for most individuals ≥ 400 mm TL (df = 1, $\chi^2 = 0.024$, $P = 0.88$).

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

Age	N	Mean TL (mm)	(SD) (mm)	Growth period (Age)	Growth increment (mm)	(SD) (mm)
0	8	7.7	(0.5)	0-1	63.5	(13.6)
1	73	71.2	(13.6)	1-2	---	---
2	1	181.0	---	2-3	---	---
3	3	232.7	(37.3)	3-4	82.0	(56.0)
4	6	314.7	(41.8)	4-5	61.5	(53.4)
5	19	376.2	(33.3)	5-6	47.9	(45.3)
6	10	424.1	(30.6)	6-7	32.2	(36.6)
7	7	456.3	(20.0)			

Table 2. Estimated annual growth increments for Colorado squawfish ≥ 400 mm TL in the Colorado River. Mean increments are from measured changes in length of recaptured fish. Length class is of fish at first capture. Growth increments with the same letter are not significantly different (ANOVA, df = 7, 94, F = 12.87, $P < 0.0001$; Fisher's LSD, $P < 0.05$). The combined average growth increment for fish 550 to 899 mm TL is also shown because mean growth increments of these sizes were not statistically different.

Length Class (mm)	N	Mean growth (mm)	(SD) (mm)
400-449	6	42.7 [a]	(8.1)
450-499	17	30.1 [b]	(18.9)
500-549	20	22.2 [c]	(13.7)
550-599	27	9.7 [d]	(8.0)
600-649	16	6.4 [d]	(6.4)
650-700	6	11.1 [d]	(8.7)
700-799	4	15.0 [cd]	(4.7)
800-899	6	3.9 [d]	(3.0)
550-899	59	8.7	(7.4)

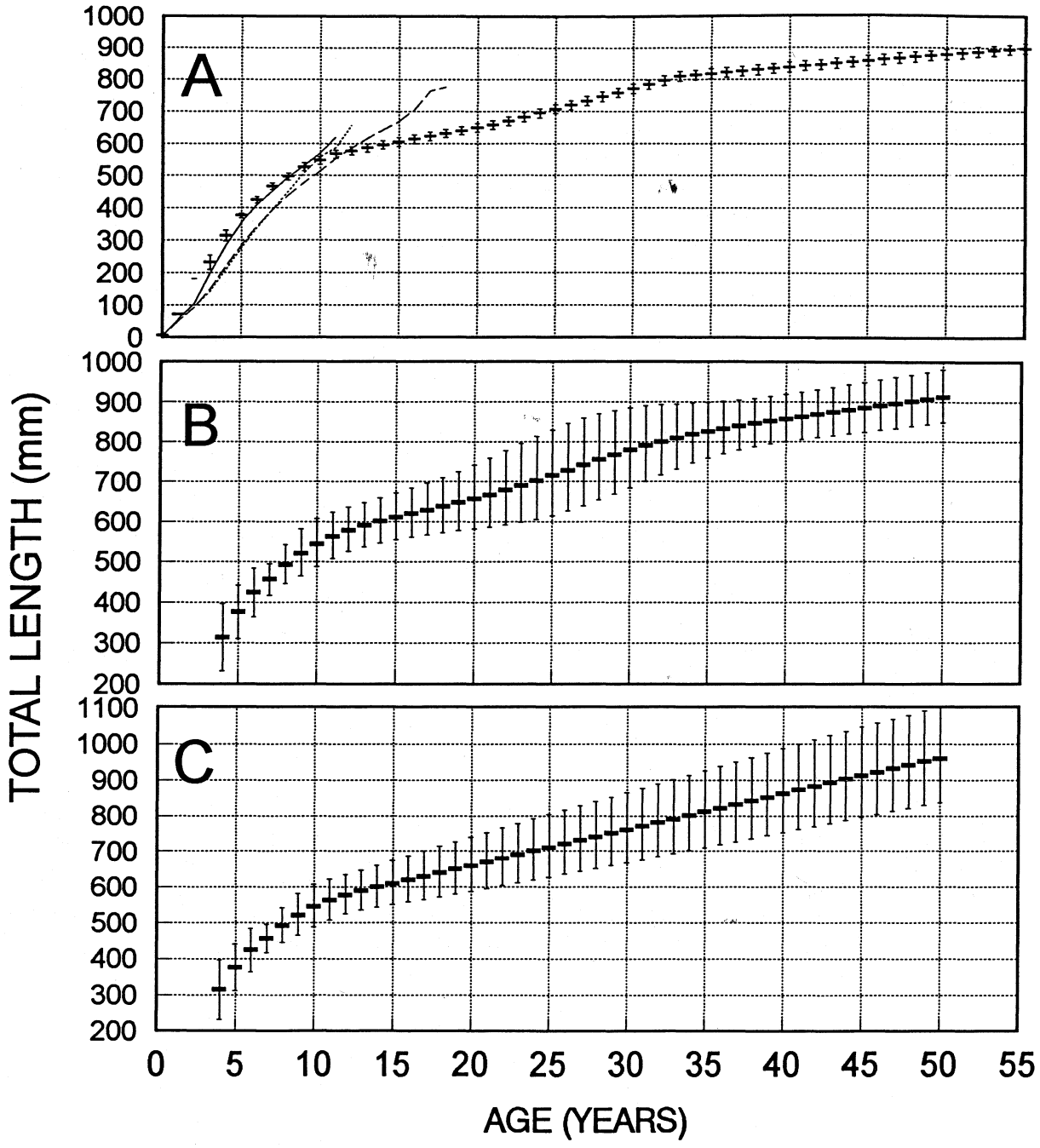


Figure 3. Estimated mean length by age for Colorado squawfish in the Colorado River. (A) Lengths calculated by four methods (see Tables 1 and 2). Bars represent +/- 1 standard error. For ages where lengths were calculated by adding mean growth increments to mean lengths of the preceding age (ages 8-55), standard errors were calculated assuming a linear combination of mean growth increments. Additional lines are growth curves reported by other researchers: solid: Seethaler (1978) for Colorado River; dotted: Hawkins (1992) for Colorado River; dashed: Hawkins (1992) for four rivers combined. (B) Lengths from Monte Carlo simulations using size-specific growth rates as shown in Tables 1 and 2. (C) Lengths from Monte Carlo simulations assuming constant growth for fish ≥ 550 mm TL (see Table 2). Bars in (C) and (B) represent the lengths of 95% of fish for each age.

Simulated length distributions produced mean lengths by age similar to those calculated by adding mean growth increments (Fig. 3a), and indicate the expected range of variation in lengths by age (Fig. 3 b). Growth increments were log-normal within size classes, and simulations were conducted using log-transformed growth rates. When growth was assumed to be constant for fish ≥ 550 mm TL, the growth rate was steady above 550 mm TL as expected, but the variance in lengths for a given age was greater than when calculated growth increments were used (Fig. 3c). The 20 simulations of length distributions conducted using different random number sequences produced nearly identical length distributions by age.

Simulations indicated there are broad ranges of ages for fish of given lengths, especially fish ≥ 550 mm TL (Fig. 4a). Individuals may take 10-22 (mean = 15) years to reach 600 mm in length; 16-30 (mean = 25) years to reach 700 mm; 20-40 (mean = 32) years to reach 800 mm. Similar, but more variable ages were found for a given length when growth for fish ≥ 550 mm TL was assumed constant (Fig. 4b).

Survival

Tests of Assumptions

No significant differences ($P > 0.05$) were found among years in the length distributions of fish ≥ 550 mm captured during 1991 through 1994 (N = 34, 41, 49, 34, respectively) in the upper reach. Similarly, no significant differences ($P > 0.05$) were found between length distributions for these years and for distributions for fish sampled in 1990 (N = 15) and 1995 (N = 44) under different sampling programs. The length distribution of fish captured in 1982 (N = 41) was significantly different from the distribution for 1992 ($P = 0.028$), but was not significantly different ($P > 0.05$) than distributions for all other years from 1990 through 1995. These results suggest that the length distribution for fish ≥ 550 mm TL was essentially stable during this period.

Catch rates, expressed as number of Colorado squawfish ≥ 550 mm TL captured per net-set, were compared for the period 1991 through 1994 (number of sets = 139, 117, 121, 105, respectively). No significant differences were found among years for the mean number of fish per net-set (Kruskal-Wallis one-way ANOVA, df = 3, $\chi^2 = 1.916$, $P = 0.590$), indicating no measurable change in abundance of fish ≥ 550 mm TL.

Differences in size distribution were found between Colorado squawfish (≥ 550 mm TL) captured with trammel nets and those captured using electrofishing. The only data set with comparable periods and regions of fish capture for both gear types was during 1994 in one section (RK 246-275) of the upper reach. The distribution of fish ≥ 550 mm TL caught with electrofishing (N = 13) contained more large fish and was significantly different ($P = 0.016$) than the distribution for fish caught with trammel nets (N = 21). A bias toward larger fish is consistent with observations made by other investigators electrofishing other species (see Reynolds 1983). Although we could not test whether distributions of fish caught with

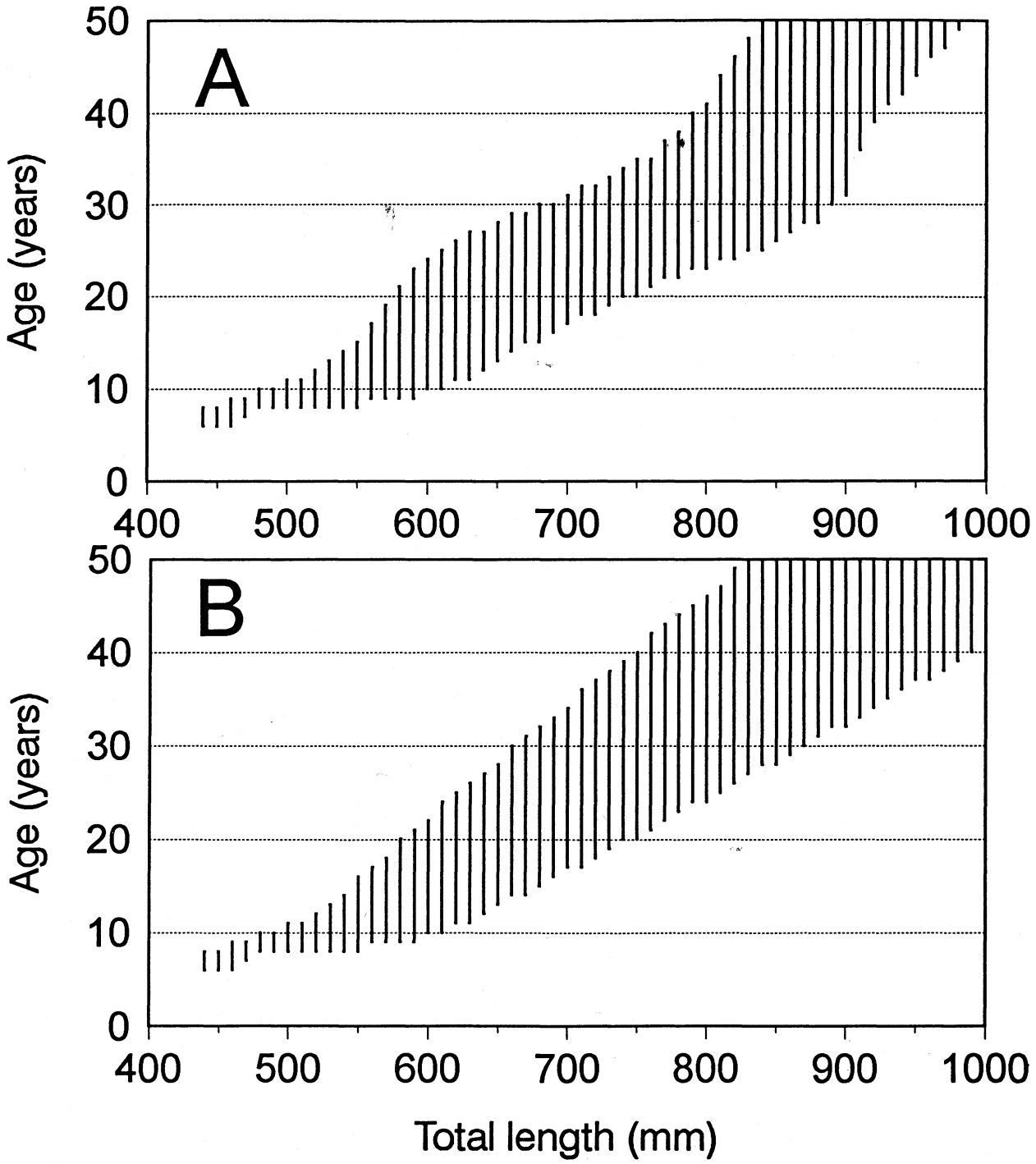


Figure 4. Simulated range of estimated ages for Colorado squawfish of given length. (A) Simulations were conducted using size-specific growth rates as shown in Table 2. (B) Simulations were conducted assuming constant growth for fish ≥ 550 mm. Bars in both graphs represent the ages of 95 % of fish of each length.

trammel nets were representative of the population, we assumed that they were because the technique actively trapped all fish in confined areas, thereby greatly reducing or eliminating the possibility for size selectivity, i.e., differential trap shyness, escapement ability, or susceptibility to electric fields. Survival estimates were therefore calculated for fish ≥ 550 mm TL using only data from fish captured with trammel nets.

Estimates

For the combined years of 1991 through 1994, suitable survival rates ranged from 0.83 to 0.88 ($P < 0.05$). Only a relatively narrow range of estimates were not significantly different from the measured distribution, even with $P < 0.001$ (Fig. 5). The best fit for the measured distribution was for a survival rate of 0.86 (Fig. 6). Similar but broader ranges of survival were estimated for individual years; these broader ranges and resulting variation among years resulted from smaller sample sizes. When data from all years were combined, a range of suitable survival rates narrowed to 0.84-0.86 (Table 3). For a theoretical population without a stable age distribution, the effect on survival rate would be a change of approximately 1 % for each percent of population increase or decrease (Table 4). Estimated survival rates were the same when growth rates for fish ≥ 550 mm TL used in the calculations of the stable length distributions varied by fish size (as shown in Table 2) or when they were assumed constant (as in Fig. 3c). The 20 simulations of stable-age distributions conducted using different random number sequences produced identical suitable survival rates, and nearly identical K-S d-value test statistics.

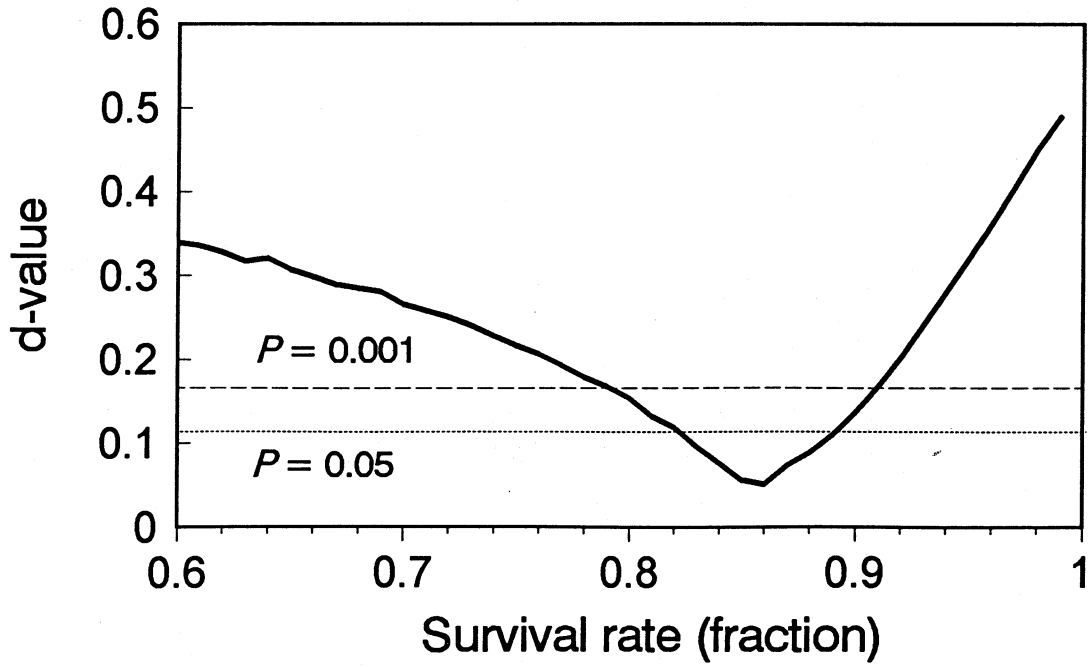


Figure 5. Kolmogorov-Smirnov d-statistic for test between stable size distributions and measured distribution for Colorado squawfish ≥ 550 mm TL captured between 1991 and 1994. Dotted lines represent the d-value for $P = 0.001$ and $P = 0.05$. Lesser d-values have lower significance levels. Examples of observed and theoretical length distributions of three survival rates and associated statistics are shown in Fig. 6.

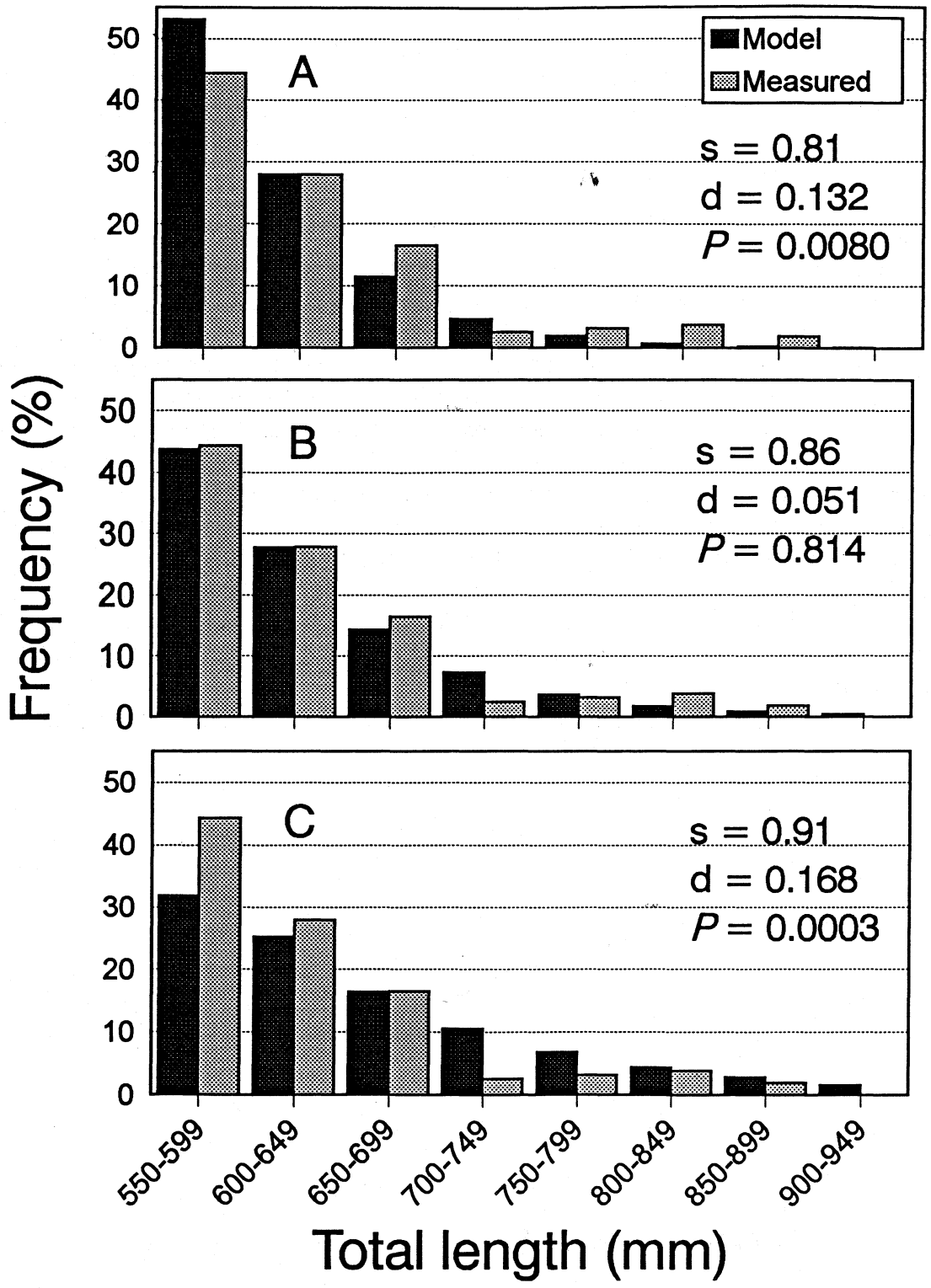


Figure 6. Stable length distributions for Colorado squawfish and measured distributions during 1991 through 1994. (A) Stable length distribution assuming survival rate (s) = 0.81; (B) s = 0.86; (C) s = 0.91. d-value (d) from K-S one-sample test and associated probability level (P) are shown.

Table 3. Survival rates of Colorado squawfish ≥ 550 mm TL for which the stable length distribution did not differ from the measured distributions (K-S one-sample test, $P > 0.05$).

Year	Survival rates
1982	0.84-0.92
1990	0.60-0.92
1991	0.82-0.95
1992	0.85-0.89
1993	0.72-0.86
1994	0.76-0.91
1995	0.74-0.88
1991-1994	0.83-0.88
all years	0.84-0.86

Table 4. Survival rates of Colorado squawfish ≥ 550 mm TL for which the stable length distribution did not differ from the measured distribution for years 1991 through 1994 (K-S one-sample test, $P > 0.05$) for annual population growth rates from -10 to 10 %. "Best estimate" is the survival rate with the smallest K-S d-value and greatest P-value.

Growth rate (%)	Survival rates	Best estimate
10	0.93-0.97	0.96
5	0.89-0.92	0.91
0	0.83-0.88	0.86
-5	0.80-0.84	0.82
-10	0.77-0.80	0.78

DISCUSSION

Growth, Age and Size

Our estimates of growth rates and mean lengths by age class were similar to those reported by Seethaler (1978) and Hawkins (1992) up to about age 8-10 (Fig. 3a); these similarities were expected given that our analysis through age 7 was also based on scales. Mean lengths at a given age were closest to those reported by Seethaler (1978), though his estimates were slightly less than ours. This may reflect differences in the annual reference point: winter for Seethaler and mid- to late spring for this study. A 13° C threshold water temperature for Colorado squawfish growth (see Osmundson 1987, Kaeding and Osmundson 1988) is generally attained in the study area during March or April. This provides 1-3 months of additional growth for fish measured during mid-April to late June compared to those with estimated lengths at annulus formation the previous winter. Results of scale analysis and additive recapture increments diverge after fish are 10 years old. Seethaler's (1978) and Hawkins' (1992) scale-based Colorado River results end at ages 11 and 12, respectively; however, Hawkins' (1992) pooled data from four upper basin rivers continues through age 18. All three of the earlier growth curves indicate high and relatively constant growth rates through the last year examined whereas our growth rates are much lower after the fish attain about 550 mm TL (Fig. 3a). We concur with Hawkins (1992) who cautioned that scale-based estimated ages are probably not reliable for Colorado squawfish beyond about age 10.

Our estimates of mean annual growth increments from recaptured adults in the Colorado River are similar to those reported by other investigators. Tyus (1988) reported that recaptured adult Colorado squawfish (N = 59; 482-770 mm TL) from the Green-Yampa rivers averaged a gain of 10.2 mm (SD = 11.3 mm) in length per year, and Hawkins (1992) reported 10-15 mm for fish > 500 mm TL from various rivers. Direct comparisons with our data are difficult because annual increments vary with fish size and the proportion of these earlier samples consisting of the faster growing small adults is unknown. However, when we pooled increments from all fish ≥ 450 mm TL (N = 121), mean annual growth was 14.4 mm (SE = 1.2 mm); from fish ≥ 500 mm TL (N = 104), 11.9 mm (SE = 1.0 mm). Thus, growth estimates from earlier studies using Carlin-tagged fish were very similar to those of our PIT-tagged fish, and suspicions of potential negative effects on growth from dangler-tags are probably unfounded. The average annual growth increment of 30 mm determined from back-calculation of scale radii as reported by Hawkins (1992) appears too high except for fish < 500 mm TL, and suggests an upper size limit for aging Colorado squawfish using scales.

Using the additive increment method to calculate mean length at each age, we noted a decline in growth rate after Colorado squawfish reached ≈ 550 mm TL, followed by a rate increase after they reached approximately 650 mm TL (Fig. 3a). Although this difference in rate was not significant, the lack of significance may have resulted from small numbers of larger (> 650 mm TL), recaptured fish. Hawkins (1992) also noted an increase in growth rate at around 650 mm TL, evidenced by both back-calculated scale data and recapture data. If this rate

increase is real, as we suspect, it suggests an increase in food availability as Colorado squawfish reach this size. Increased gape size, or more effective foraging and handling abilities may allow utilization of larger and more abundant prey.

While there is much variation in growth among individual fish, it appears that in successive years most fish do not grow consistently faster or slower than the average and average growth rates do not differ greatly among years. Nevertheless, there can be large differences among individuals in time it takes to reach a given length: there was a 20-year range of potential ages for a given length for fish > 800 mm TL. Although length is therefore a rather imprecise indicator of age, we can conclude that the largest fish present in the population are quite old. For individuals 900 mm long, 34 years might be a minimum age, but an average age would likely be 47-55 years (Fig. 3 a and b). These fish are very rare: of approximately 1,080 subadult and adult Colorado squawfish captured from the Colorado River during 1979-1995 only three have been > 900 mm TL (0.28%) and two of these were < 905 mm TL. The largest, captured in 1990 by UDWR biologists, was 960 mm TL, considerably larger than any other reported from upper basin rivers (McAda et al. 1994).

There are numerous anecdotal accounts of Colorado squawfish historically reaching lengths of 1,200-1,800 mm TL (e.g., Quarterone 1993), far larger than any found during the past 20 years. Two explanations for the disappearance of such large individuals have been proposed: 1) growth rate has declined (Behnke and Benson 1983), and 2) survival rate has declined (Gilpin 1993). Behnke and Benson (1983) suggested that extirpation of the bonytail (*Gila elegans*) impacted the food supply of Colorado squawfish. Gilpin (1993) showed, through simulations, that average and maximum fish size would significantly increase if adult survival rate was increased to 0.95, and suggested that rates may have declined due to angling mortality. However, neither hypothesis adequately explains the disappearance of very large individuals. Kaeding and Osmundson (1988) concluded that slow growth in the upper basin was the historic norm because temperature regimes of mainstem rivers have, with few exceptions, remain unchanged and potential foods, *Gila spp.* and native suckers, remain plentiful. Also, the size structure of Gilpin's simulated population with a survival rate of 0.95 indicated that the largest individuals would still be < 1,000 mm long.

Though the preceding two explanations may explain in part the reduction in average and maximum size, we offer a third hypothesis: very large fish may have attained their size while residing in the Lower Colorado River Basin (downstream of Lee's Ferry) and moved upstream later in life where they were eventually captured. Kaeding and Osmundson (1988) demonstrated that longer growing seasons and warmer temperatures in the lower basin during historic times would have provided 1.5-2.3 times the annual thermal units for growth than that in upper basin reaches. Additionally, Colorado squawfish are capable of making long-distance movements; radio-tagged adults have been documented traversing the entire length of their current range in the upper Colorado River (313 km) in less than 3 months (McAda and

Kaeding 1991). If the lower basin was once the source of the upper basin's large fish, as we suggest, subsequent blockage of upstream movement by the construction of mainstem dams and the eventual extirpation of lower basin populations might explain the disappearance of such large individuals in recent times.

Survival

The range of suitable ($P < 0.05$) survival estimates of 0.83-0.87 (1991 through 1994 data) was higher than that calculated by Gilpin (1993) for the Green River population (0.81) and may reflect differences in environmental factors between the two rivers. However, had Gilpin's (1993) methodology provided a range of estimates rather than a point estimate, his range may have overlapped ours, suggesting no differences in survival rates between the two rivers. Also, deviations from a stable population size in either river would affect the comparability of these estimates since both were based on the assumption of stable population size. Other differences in methodologies or assumptions may explain some of the difference in estimated rates.

The method used to determine survival rate in this study was not designed to replace currently available capture-recapture models for open populations such as Jolly-Seber (Jolly 1965, Seber 1965) and variations thereof. However, it can be applied when consistent capture effort and long capture histories necessary for the Jolly-Seber model (see Pollock et al. 1990) are not available. Chief limitations of the method used here are the need for population structure information over several years (to determine if age distribution is stable), and capture methods that sample various-sized fish at rates representative of the actual population. Tests indicated that population size structure of Colorado squawfish ≥ 550 mm TL in the Colorado River did not change significantly from 1990 through 1995 and was similar to that in 1982. We were not able to test for capture bias in trammel nets, but disproportionate numbers of large fish caught with electrofishing gear was consistent with known biases of this gear type (Reynolds 1983). When fish captured by electrofishing were included in the analysis, estimated survival rates increased as expected (not shown).

Though historic survival rates are unknown, there are some new sources of mortality that may have lowered rates during recent times, while other sources have probably changed little. Accidents during high water events (abrasions, strandings, etc.), stress-related factors during spawning, and avian predation by great blue herons (*Ardea herodias*) and bald eagles (*Haliaeetus leucocephalus*) have likely always been primary sources of adult mortality. Significant change in mortality rates from these factors is unlikely except perhaps that the frequency of strandings may have increased in recent times because of the excavation of numerous gravel-pit ponds along the floodplain of the upper reach. Colorado squawfish are attracted to these habitats when ponds flood during spring runoff and strandings have been documented (FWS unpublished data) when declining flows later re-isolate the ponds. Substantial angling and netting activities of settlers and residents from the 1890's through the

1950's (see Quarterone 1993) likely boosted mortality rates, though harvest by aborigines during seasons when the fish were concentrated may also have been significant during prehistoric times. Anglers today fish for the introduced channel catfish (*Ictaluras punctatus*), but mortality from incidental catches of Colorado squawfish still occur, particularly in the Grand Valley where the river is surrounded by an urban area (FWS unpublished data). Trammel et al. (1996) conducted creel surveys along portions of the Colorado River in Utah and concluded that angling-related mortality of Colorado squawfish there was probably insignificant. While the significance of angler-related mortality in the Grand Valley is unknown, it has probably been greatly reduced during the past 20 years from educational efforts and the penalties associated with harming a protected species.

New mortality factors to which Colorado squawfish may be subjected include parasitic diseases and problems encountered with ingestion of channel catfish. While some parasitic diseases have been introduced, none are believed fatal (Seethaler 1978, Flagg 1982) and little additional mortality would be expected. Numerous fishermen have reported finding dead Colorado squawfish containing channel catfish with the spines extended and lodged in the pharynx or esophagus (Vanicek and Kramer 1969, Quarterone 1994). The probability of encountering any dead squawfish is very low; the fact that several have been reported with catfish in their throats suggests this is not an uncommon occurrence. McAda (1983) and Pimentel et al. (1985) reported extracting channel catfish from the mouths of live Colorado squawfish. During our study, several large Colorado squawfish were observed with perforations or slits in the gular region, suggesting past encounters with the spines of ingested channel catfish. Because channel catfish are abundant and ubiquitous, the likelihood of a long-lived piscivore eventually eating one is probably high; consequently, we suspect this is a significant source of mortality.

Gilpin's (1993) population viability analysis (PVA) on the Green River population of Colorado squawfish identified information gaps that if filled would strengthen future PVA or other population assessments dependent on demographic analysis. Growth and survival rates were important parameters for which he identified the need for more accurate estimates. This work is a step toward fulfilling that need.

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NON-SPAWNING MOVEMENTS OF SUB-ADULT AND ADULT COLORADO SQUAWFISH IN THE UPPER COLORADO RIVER

FINAL REPORT

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EXECUTIVE SUMMARY

Colorado squawfish (*Ptychocheilus lucius*), a large piscivorous cyprinid endemic to warm-water reaches of the Colorado River system, is well known for its spawning migrations and long-distance drift of resulting larvae. However, little is known about the dispersal movements of juveniles recruiting to the adult population. Our objective was to describe these movements among Colorado squawfish in the upper Colorado River in an attempt to better understand the life history strategy of this endangered species.

River-wide, capture-recapture data of PIT-tagged fish were used to document movements of subadult and adult Colorado squawfish. Capture and tagging efforts were made during spring runoff (mid-April to mid-June) from 1990 through 1995. Most captures were made by trammel-netting flooded backwaters, but data were also supplemented with electrofishing captures. Limited capture and tagging efforts were made in 1990 and only in the upper reach (upstream of Westwater Canyon). During 1991-1994, three passes through the upper reach were made each year to net Colorado squawfish; with each pass, every backwater was netted. Two such passes were made each year through the lower reach (downstream of Westwater Canyon), with only one pass made during 1991. Recapture data obtained during 1995 was from other electrofishing and netting studies conducted in both reaches.

Longitudinal distribution of Colorado squawfish was described in terms of mean size of fish and mean number of adults captured per net in six river strata. Concentration areas of Colorado squawfish during the spring runoff period were also noted. Movements of fish captured one year and recaptured in a subsequent year were compared among size classes of fish and between those fish initially captured in the lower reach and those captured in the upper reach. Sizes of those fish moving from the lower reach to the upper reach were also noted. After hypothesizing that dispersal movements are a response to food resource gradients, we compared relative body condition of similar-sized adults from the lower and upper reaches and compared relative abundance of native forage fish among river strata.

Average length of Colorado squawfish progressively increased upstream and was most pronounced during the first years of the study. During 1991-1992, most adults (> 500 mm TL) were concentrated in the upper reach and very few adults were found in the lower reach. As the study progressed, demographics changed as 2-3 consecutive strong year classes, hatched during the mid-1980's, grew and dispersed as they recruited to the adult population. As a result, average length increased in lower-reach strata and decreased in upper-reach strata. By 1993, there was a five-fold increase in catch rates of adults in the lower reach. Lower-reach sites where subadults and adults were most concentrated during runoff included the mouths of Indian and Kane Springs creeks in Stratum 1, and Cisco and Sagar's washes in Stratum 3. Concentration sites for adults in the upper reach during runoff included

backwaters at the Walter Walker Wildlife Area (Stratum 6), two sites across the river from one another in the 15-mile reach (Stratum 7), and Knowles Canyon (Stratum 5).

Of those Colorado squawfish initially captured and tagged in the upper reach, 16% were later located > 10 km from the previous capture site. Of these movements, 80% were directed upstream. None of the fish located in the upper reach during the study period were later recaptured in the lower reach. Of those fish tagged in the lower reach, 58% were later located > 10 km from the previous site; 68% of these displacements were directed upstream. Over the five-year period, 44% of movements > 10 km were from the lower reach to the upper reach, and the proportion of these between-reach movements increased each year. Distance moved was inversely related to fish size, i.e., distance moved decreased with increased fish size. Displacement of fish < 550 mm TL averaged 33.6 km; for those > 550 mm TL, average displacement was only 7.5 km. The smallest fish we documented moving from the lower to the upper reach was no longer than 449 mm, and the largest fish was at least 570 mm long.

Movement of young adult Colorado squawfish was likely a response to their changing food requirements as they grew and matured. A net shift in abundance to upstream reaches was probably because upstream movements were rewarded with greater food availability. Two lines of evidence supported this hypothesis: 1) Catch rates of roundtail chub (*Gila robusta*) and bluehead (*Catostomus discobolus*) and flannelmouth sucker (*C. latipinnis*), likely prey of adult Colorado squawfish, were significantly higher in the upper reach than in the lower reach, and 2) body condition of Colorado squawfish decreased with fish size in the lower reach but increased with fish size in the upper reach.

Our results suggest that young Colorado squawfish move more than older ones and that upon arrival to the upper reach they move less. Evidently, older fish establish home feeding ranges in areas they have found to be most productive and have little need for further exploratory movements. The reach upstream of Westwater Canyon evidently provides the best adult feeding opportunities in the upper Colorado River. If reproduction and recruitment rates, currently limiting Colorado squawfish numbers in the Colorado River, can be increased, improved forage availability in existing reaches and passage to historic reaches would help provide for an expanding adult population.

INTRODUCTION

Understanding the life history of the endangered Colorado squawfish (*Ptychocheilus lucius*) is prerequisite to developing strategies for its recovery. Endemic to the Colorado River basin, this species is noted as the largest cyprinid native to North America. The historic range of this piscivore has been reduced by 80% (Tyus 1990). Extant populations occur only in the upper Colorado River basin (i.e., upstream of Glen Canyon Dam) in warm-water reaches of the Colorado, Green and San Juan river systems. The species has integrated movements into its life strategies, including annual, potamodromous, spawning migrations (e.g. Tyus and McAda 1984, Tyus 1985, Tyus 1990, McAda and Kaeding 1991), and the subsequent downstream drift of emerging larvae (e.g. Haynes et al. 1984, Nesler et al. 1988, Tyus 1990, Tyus and Haines 1991).

Upon emergence, Colorado squawfish larvae drift downstream and are soon widely distributed. By late summer they can be collected with seines from backwaters and other low-velocity habitats where they largely remain through the postlarval phase (Haynes et al. 1984, Tyus and Haines 1991, McAda and Kaeding 1991). By fall, many young-of-the-year (YOY) in the Colorado River become concentrated in the lower 103 km (above the Green River confluence) where gradient is low and sand-bar-formed backwaters are most plentiful (Valdez et al. 1982, McAda et al. 1994). There they rear through the first year of life. After attaining about 100 mm in length, Colorado squawfish are infrequently collected; however, once > 250 mm long, they become more susceptible to capture with trammel nets and electrofishing.

Size of Colorado squawfish in the Colorado River varies longitudinally: early life stages are found primarily in the lower reaches and adults are found primarily in more upstream reaches (Valdez et al. 1982, Osmundson and Burnham 1996). This differential distribution of life stages was also noted in the Green River system by Tyus (1986) and Tyus et al. (1987). Valdez et al. (1982) suggested that: "... YOY move downstream with age, and juveniles and adults subsequently move upstream with increasing age." Tyus (1986), in reference to the Green River population, similarly noted that : "A net long-term movement of juveniles must occur to populate adult areas upstream, probably in the late young-adult stage,..." These distributional patterns of various life stages of Colorado squawfish indicate that population dynamics occur at the landscape scale and that large sections of river are needed to meet the needs of all life stages in a given population. Evidently, the best spawning habitat occurs in middle to upper reaches. Long-distance drift provides a mechanism for delivering emerging larvae from these areas to more optimum nursery habitat, generally located far downstream (Tyus 1990).

Though hypothesized, patterns of river-wide dispersal of adults and subadults from downstream areas where they reared to upstream reaches has not been documented and is poorly understood. Our primary objectives were to describe the distribution of subadult and adult Colorado squawfish in the Colorado River and document their dispersal patterns. We

hypothesized that upstream movement of young adults is a response to resource gradients. More specifically, we hypothesized that upstream dispersal results from individuals seeking foraging areas more likely to meet the changing food requirements of a growing piscivore. Hence, we also investigated spatial variation in Colorado squawfish body condition and abundance of likely forage species.

STUDY AREA

Our study area included the entire portion of the upper Colorado River occupied by Colorado squawfish, from the downstream confluence with the Green River in Utah upstream to the Grand Valley Diversion Dam at Palisade, Colorado. It also included the lowermost 3.5 km of the Gunnison River, between Redlands Diversion Dam and the confluence with the Colorado River (Fig. 1). Colorado River locations described herein are in river kilometers (RK) from the Green River confluence (RK 0.0) and are conversions of river miles mapped by Belknap and Belknap (1974). Based on the distributional pattern of adults and juveniles, the study area (Fig. 1) was partitioned into a lower reach that extended from RK 0.0 upstream to the lower end of Westwater Canyon (RK 181.0), and an upper reach, from the upper end of Westwater Canyon (RK 200.0) to RK 298.1, the upstream terminus of the study area. Westwater Canyon, a 19-km section dominated by large rapids and turbulent eddies, was excluded for logistical reasons and because past studies have indicated few Colorado squawfish are found there (McAda and Kaeding 1991).

METHODS

Distribution and movement

To document distribution of Colorado squawfish, we systematically captured individuals from throughout the study area over a four-year period (1991-1994). The river was divided into seven strata based on major changes in average channel gradient (Fig. 1); our study area consisted of three strata upstream and three downstream of Westwater Canyon (Stratum 4). The distribution of various sizes of Colorado squawfish was examined by comparing mean lengths of captured fish among river strata using standard ANOVA and the Tukey-Kramer multiple-comparison test. We also used a T-test to make between-year comparisons of mean length within strata. To measure movements of Colorado squawfish, locations of first and subsequent captures of tagged fish were compared.

Our primary capture method was to set trammel nets in backwaters, flooded ponds and flooded canyon mouths because these calm habitats were known to attract Colorado squawfish during the spring runoff period (Osmundson and Kaeding 1989). We began

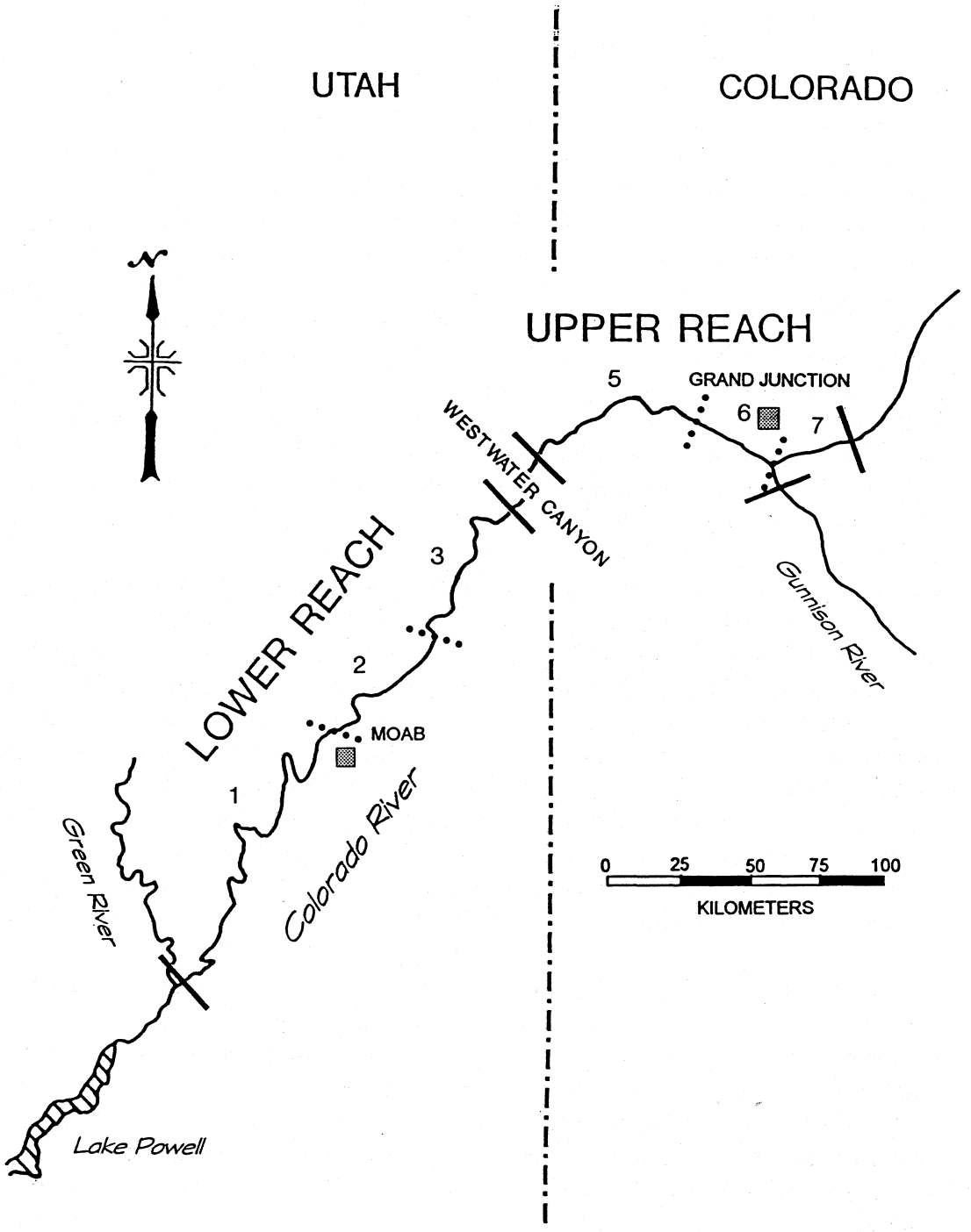


Figure 1. Map of the study area. The lower boundary is the Green River confluence (lower black line). Upper and lower study reaches are separated by Westwater Canyon marked with black lines. Black lines also mark the upper ends of the study area on the Colorado River and 3.5 km up the Gunnison River where diversion dams blocked upstream movement of fish during the study period. Dotted lines demarcate the six study strata (numbered).

tagging Colorado squawfish in the upper reach (see Fig. 1) in spring of 1990 but did not conduct systematic searches. Beginning in 1991, three passes through the upper reach were made each spring. With each pass, we netted every backwater that might contain subadult or adult Colorado squawfish. A pass generally took 7-9 days to complete. Capture and tagging efforts in the lower reach began in 1991. There, one pass was made the first spring and two passes each spring during 1992-1994. In some portions of both reaches where backwater habitats were rare, shorelines were electrofished with a 5-m, electrofishing boat equipped with a variable voltage pulsator (Coffelt VVP-15) using pulsed DC current.

Captured Colorado squawfish were scanned for the presence of a passive integrated transponder (PIT) tag. If none was found, we implanted a PIT tag (Biomark, Inc., Boise, Idaho) in the body cavity using a hypodermic needle after fish were anesthetized with Tricane methanesulfonate. The insertion site for the tag was 2-5 mm posterior to the base of the left pelvic fin. Maximum total length (TL), as defined by Anderson and Gutreuter (1983), was measured (+/- 1 mm). Fish were weighed with an electronic balance (+/- 1 gram) and released after recovery from the anesthetic.

We compared movement patterns among 100-mm size groups of Colorado squawfish and between those fish initially captured in the lower reach and those initially captured in the upper reach. To differentiate between localized movements and more substantial dispersal movements, we used as a criterion an arbitrarily defined minimum distance between capture sites: a distance < 10 km was considered a localized movement; a distance ≥ 10 km a dispersal movement. Data from previous radiotelemetry studies indicated that most adults moved < 7 km during the non-spawning period (USFWS unpublished data). To compare mean distance displaced among size classes of fish, we used ANOVA on *ln* transformed data (transformations were made to equalize variance within cells), and made multiple comparisons (Tukey-Kramer test). Comparisons between percentages of upstream and downstream movements were made using test-of-proportions.

For the movement analyses, only displacements one or more years apart were used; no within-year capture-recapture data were used. This allowed fish adequate time to disperse between captures. Also, captures during spawning periods and during pre- and post-spawning migratory periods were excluded so that temporary spawning movements would not be confused with dispersal movements. Sampling was conducted from mid-April to mid-June during spring run-off. Concurrent radiotelemetry studies indicated that annual spawning movements did not commence until late June. The exception to this was 1994 when Colorado squawfish moved to spawning locations in mid-June, presumably due to early warming of water from unseasonably low water conditions. Thus, fish marked or recaptured in 1994 during the month of June were excluded from the analyses. During other years, captures through June 16 were included.

Colorado squawfish capture data from other studies were also included in our analyses when they met our criteria. Additional capture data from Stratum 5 was provided by Colorado

Division of Wildlife (CDOW). Utah Division of Wildlife Resources (UDWR) provided capture data on individual fish from the lower reach that FWS had either initially captured or subsequently captured. Both CDOW and UDWR conduct annual electrofishing surveys of the river during April and May as part of the Interagency Standardized Monitoring Program (ISMP). Capture data from the lowermost 3.5 km of the Gunnison River were supplemented with those from a concurrent FWS electrofishing survey of that river (see Burdick 1995).

Though no systematic, river-wide searches for marked fish were made during 1995, we utilized recapture data available from other surveys. This data was from four sources: lower Gunnison River surveys, a FWS survey of ponds near RK 263 in the Walter Walker Wildlife Area (see Mourning 1995), and the aforementioned ISMP surveys by CDOW and UDWR.

Body Condition

Relative body condition (*Kn*) was calculated for each fish for which we had lengths and reliable weights (those measured with an electronic balance). As noted by Hawkins (1992), relative condition (*Kn*) is a better statistic than is the more widely used Fulton's condition factor (*K*) because relative condition is comparable between fish of different lengths; Fulton's condition factor does not account for allometric growth and therefore varies by fish length making comparisons among sizes inappropriate (see Le Cren 1951). Relative condition is the observed mass 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:

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

Because Hawkins (1992) showed that Colorado squawfish condition changes monthly, we first developed mass-length relationships specific to the month during which the fish were captured. Though Hawkins provided weight-length regression coefficients for Colorado squawfish captured from the Colorado River during 1978-1989, we used our own data to derive new coefficients because 1) our monthly sample sizes were larger, 2) we used juvenile as well as adult sized fish (≥181 mm TL as opposed to ≥ 428 mm TL used by Hawkins), and 3) our weights were presumably more accurate (because of the use of a balance as opposed to spring scales that were widely used in the past).

We calculated mass-length relationships separately for the months of April, May and June using 1990-1994 capture data. Only fishes weighed with an electronic balance were included. Excluded from the June calculations were 1994 data because early gonadal maturation that

year may have resulted in abnormally high condition factors. Slope and intercept coefficients were derived by regressing log-transformed mass as a function of length.

Condition of each fish was calculated by using month-specific constants. For instance, the condition of a fish captured in April was relative to that of the average fish captured in April, not relative to fish captured in other months. This allowed us to make condition comparisons between areas that might otherwise be biased by the differences in proportions of fish caught in various months. Bias could result if condition factors were calculated using constants from one weight-length regression derived from all spring or all annual captures. For example, if fish in June had a higher condition factor than those in April or May, average condition within a reach where there was a higher proportion of June-captured fish would likely be higher than other reaches where proportions of June-captured fish were lower.

After condition factors for individual fish were calculated, data were partitioned by reach (upper and lower) and by 100-mm length classes. Again, fish not weighed with an electronic balance and those captured in June 1994 were excluded. We used a T-test to test for differences between lower and upper reach fish (within 100-mm length classes), and ANOVA and the Tukey-Kramer multiple comparison test to compare condition among length classes within reaches.

Relative Abundance of Forage Fish

Electrofishing and trammel-netting catch rates were used as an index of relative abundance of larger-sized (> 100 mm TL) forage fish. Relative abundance among strata of small minnows (*Notropis, Pimephales* etc.), the likely forage for young Colorado squawfish, was not investigated.

For electrofishing surveys, two or more 0.8-km sample reaches were randomly selected within each stratum. To determine number of sample reaches for each stratum, total miles within the stratum was rounded up to the next 10-mile increment and divided by 10. Thus, a 14-mile-long stratum had two sample reaches; a 28-mile-long stratum, three. Reach locations within strata were determined by using a random numbers table to select the river-kilometer (to the nearest 0.1 km) of the upstream end of each reach. Electrofishing gear was the same as described before. Within each 0.8-km-subreach, both shorelines were electrofished in a downstream direction. Total shocking time for each shoreline was recorded in seconds by an automatic counter on the VVP. Each shoreline within each subreach was treated as a separate sample, resulting, for example, in four electrofishing samples for a stratum with two 0.8-km subreaches. Species and total length of each captured fish was recorded; fish were then released at the lower end of the subreach. Sampling was conducted from 20 April through 7 July, 1993. Catch-per-unit-effort (CPUE) was calculated by dividing the total number of fish (by species) by total shocking time for each electrofishing sample; values for all samples within a stratum were averaged to provide mean CPUE for that stratum.

Table 1. Locations of sample reaches within Colorado River strata sampled for Colorado squawfish native food fishes. Locations are described as river-kilometers upstream of the confluence of the Green River. Stratum No. 4 was not sampled (see text).

Stratum No.	Ave Gradient (m/km)	Strata locations (km)	Reach No.	Reach locations (km)
01	0.21	0.0-112.6	1	5.2-6.0
			2	12.2-13.0
			3	20.9-21.7
			4	30.1-30.9
			5	61.6-62.4
			6	100.6-101.4
			7	103.5-104.3
02	1.33	112.6-140.6	8	121.3-122.1
			9	129.0-129.8
03	0.61	140.6-181.0	10	148.5-149.3
			11	156.6-157.4
			12	172.2-173.0
04	2.42	181.0-200.0	-	-
05	0.91	200.0-245.5	13	212.9-213.7
			14	228.0-228.8
			15	234.6-235.4
06	1.27	245.5-275.1	16	252.9-253.7
			17	270.0-270.8
07	1.70	275.1-298.1	18	287.2-288.0
			19	293.8-294.6

Trammel-net CPUE, the mean number of each species caught per net set, was also summarized by strata. Netting data were from the nets set for Colorado squawfish as described above. Collection of netting data for fishes other than Colorado squawfish began in 1992 and continued through 1994. Numbers of each species per net was recorded; except for Colorado squawfish, lengths of trammel-netted fish were not taken.

To develop an overall index of relative abundance of native fish, we pooled within each sample the number caught of the three common species, bluehead sucker (*C. discobolus*), flannelmouth sucker (*Catostomus latipinnis*), and roundtail chub (*Gila robusta*). Because of the deep bodies of common carp (*Cyprinus carpio*) and the spines of channel catfish (*Ictaluras punctatus*) these two species were assumed to be largely unavailable as forage items for Colorado squawfish. We assumed white suckers were available because, like native species, they are soft rayed and fusiform shaped. However, we analyzed these separately.

For a separate analysis, we assumed that because of their large size, many adult fish were not vulnerable to predation by Colorado squawfish. We therefore partitioned out the larger size classes and then compared catch rates among strata. The maximum size of prey fish a given size of Colorado squawfish can consume is unknown. For fusiform-shaped prey, maximum size is probably not limited by predator gape width but rather by prey body length or mass. To get a rough idea, we assumed Colorado squawfish could consume prey half their own length, and therefore fish < 300 mm TL would be vulnerable to predation by many adult Colorado squawfish. In calculating catch rates, we pooled numbers of all species, native and nonnative, with the exception of channel catfish. Comparisons of catch rates among strata for this and the previous analysis were made using ANOVA on *ln* transformed data and the Tukey-Kramer multiple comparison test.

RESULTS

Distribution

Fish Size

Average length of Colorado squawfish progressively increased upstream (Fig. 2). Because samples from strata 2, 3 and 5 were small, lengths of 1991- and 1992-captured fish were pooled and those from 1993- and 1994-captured fish were pooled. For the 1991-1992 period, mean lengths from strata 3, 5, 6 and 7 were higher than those from Stratum 1; those from strata 5, 6, and 7 were higher than those from Stratum 2; those from Stratum 7 were higher than those from Stratum 3 ($P < 0.05$).

During 1993-1994, differences among strata were not so pronounced. Mean lengths of fish from strata 3, 5, 6 and 7 were only significantly higher than that of Stratum 1 fish ($P < 0.05$). Average sizes of fish captured in the lowermost two strata were larger during 1993-1994 than during 1991-1992 ($P < 0.0001$). In upper-reach strata, mean lengths apparently declined between 1991-1992 and 1993-1994; though only significantly so in stratum 7 ($P = 0.012$).

Adult Numbers

Netting catch rates provided some insight into river-wide differences in adult relative abundance, but we exercised caution in their interpretation. Differences in densities of fish among strata were likely influenced by the number of 'nettable backwaters' in a given stratum. For example, because backwaters are sought out by Colorado squawfish during high water, adults may be disproportionately concentrated in the few backwaters that exist in strata where backwaters are rare resulting in higher catch rates than strata with many backwaters. Also, due to low numbers of net sets, there was high catch rate variability in strata where backwaters were rare, especially in strata 2 and 3. To partially overcome this problem, sample size was increased by pooling netting data from all strata within the lower reach and from all

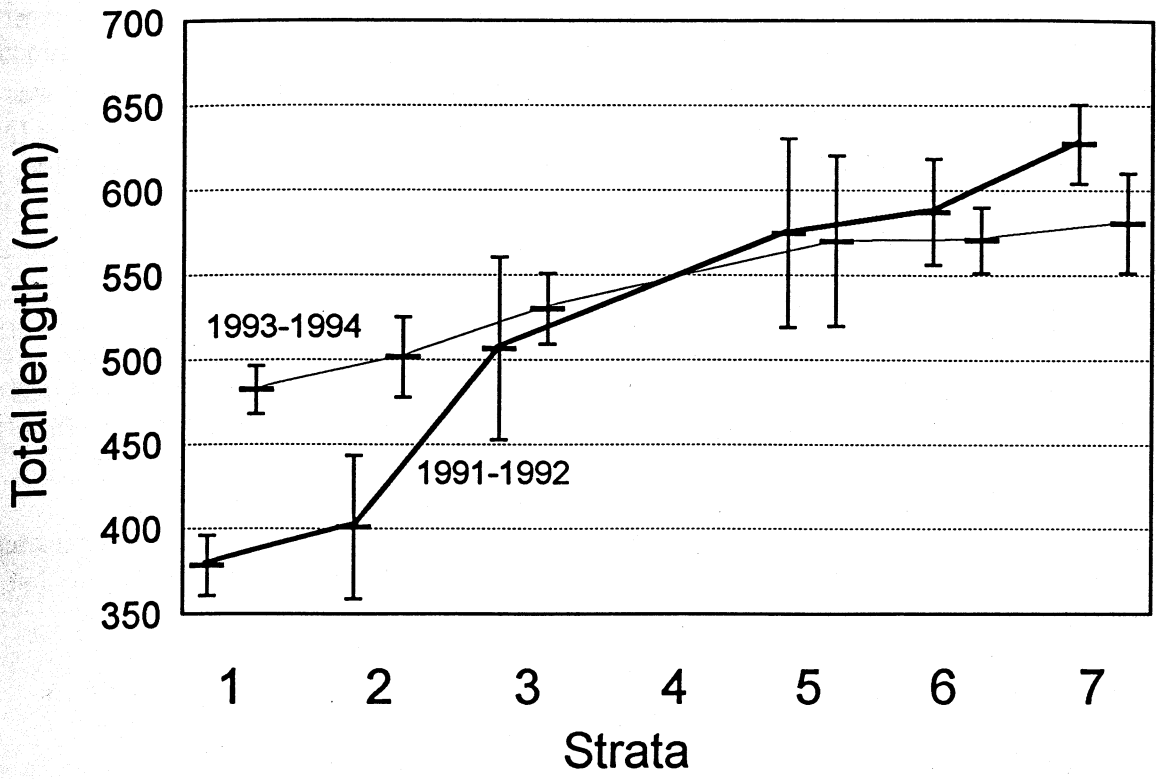


Figure 2. Mean length of Colorado squawfish by stratum. Lengths from fish captured in 1991 and 1992 (heavy line) and those captured in 1993 and 1994 (light line) were pooled. Error bars represent 95% confidence intervals.

strata within the upper reach and restricting comparisons to those between upper and lower reaches rather than among strata. A better use of the netting catch-rate data was in making among-year comparisons within reaches.

Netting catch rates indicated that adult distribution changed during the four-year period of study. In 1991, prior to recruitment of the strong year classes produced during the mid-1980's (see Osmundson and Burnham 1996), very few adult Colorado squawfish inhabited the lower reach. During the 1991 netting efforts, no Colorado squawfish > 500 mm TL were found in stratum 1 or 2 and only one was captured in Stratum 3; this resulted in an overall mean CPUE of 0.02 (SE = 0.02) adults per net in the lower reach (N = 47 net sets). In contrast, 42 were captured during our netting efforts in the upper reach, resulting in a mean CPUE of 0.30 (SE = 0.07) adults per net (N = 139). A similar pattern was evident in 1992; no Colorado squawfish > 500 mm TL were captured in Stratum 1 or 2, though six were captured in Stratum 3. Mean CPUE of adults > 500 mm TL was 0.13 (SE = 0.09) fish per net (N = 49) in the lower reach and 0.46 (SE = 0.09) fish per net (N = 114) in the upper reach.

By 1993, many individuals from the mid-1980's year classes had grown to lengths > 500 mm thereby significantly changing adult demographics. Adult-sized Colorado squawfish were captured in nets set in strata 1 (17 caught) and 2 (two caught) for the first time. In the lower reach, mean CPUE for individuals > 500 mm TL increased to 0.20 (SE = 0.04) fish per net (N = 115). In the upper reach, 1993 CPUE of adults was 0.57 (SE = 0.10; N = 115). In 1994, catch rates were generally similar to those of 1993.

Concentration Areas for Subadults and Adults

Subadult and adult Colorado squawfish were often patchily distributed during the spring sampling period. In Stratum 1, during 1991, Colorado squawfish (subadults) were captured in only 16% of the backwaters sampled (Tables 2 and 3) and 88% of the captures were from two sites: the mouth of Indian Creek at RK 26.5 (55%) and the mouth of Kane Springs Canyon at RK 93.6 (33%). After 1991, subadults appeared to be more dispersed; we captured fish in 23-45% of the backwaters sampled and the most caught in any one backwater comprised 26-46% of the total caught. The mouth of Kane Springs Canyon was the site that yielded the most captures in 1993 (26%) and 1994 (28%).

In strata 2, 3 and 5, patterns were difficult to discern because of the paucity of backwaters. This was particularly true for Stratum 2. The mouth of Salt Wash (RK 120.7) yielded the only captures in two of the three years Stratum 2 was sampled. For Stratum 3, 22-42% of the backwaters sampled yielded Colorado squawfish; Sagar's Wash (RK 159.3) yielded the most (78%) in 1992 and Cisco Wash (RK 161.2) yielded the most in 1993 (37%) and 1994 (89%). In Stratum 5, backwaters suitable for netting Colorado squawfish were more abundant during 1991 than in subsequent years (Table 2). Deposits of silt in the mouths of many backwaters not only blocked netting efforts but also limited entry by Colorado squawfish. The mouth of Knowles Canyon (RK 216.1) yielded the most captures (46%) in 1991.

The highest number of backwaters per kilometer was in Stratum 6 and Colorado squawfish were captured in 26-34% of the backwaters sampled there. Captures from flooded ponds in the Walter Walker Wildlife Area were 37%, 78% and 58% of all captures in Stratum 6 during 1992, 1993, and 1994, respectively.

Stratum 7 had the second highest number of backwaters per kilometer and Colorado squawfish were captured in 29-50% of the backwaters sampled there. Captures from a backwater on the Griffith property at RK 282.1 comprised 35-52% of the total captures during 1991-1993. A backwater across the river from the Griffith property (RK 282.4) had the most captures (39%) in 1994.

Table 2. Numbers of sampled backwaters (BA), nets set, and Colorado squawfish (CS) captures, by stratum and year. Captures by electrofishing are not shown.

	Year			
	1991	1992	1993	1994
Stratum 1				
Different backwaters sampled	32	22	33	45
Total nets set	36	31	100	101
CS captures	33	13	47	40
Backwaters with CS captures	5	5	15	14
Highest captures from one BA	18	6	12	11
Stratum 2				
Different backwaters sampled	1	4	3	-
Total nets set	1	6	7	0
CS captures	2	4	2	-
Backwaters with CS captures	1	2	1	-
Highest captures from one BA	2	3	2	-
Stratum 3				
Different backwaters sampled	10	7	12	7
Total nets set	10	12	37	9
CS captures	3	9	19	9
Backwaters with CS captures	3	2	5	2
Highest captures from one BA	1	7	7	8
Stratum 5				
Different backwaters sampled	20	12	11	11
Total nets set	42	16	19	17
CS captures	13	2	4	2
Backwaters with CS captures	5	1	2	2
Highest captures from one BA	6	2	3	1
Stratum 6				
Different backwaters sampled	23	29	26	27
Total nets set	44	55	52	42
CS captures	12	30	50	40
Backwaters with CS captures	7	10	8	7
Highest captures from one BA	5	11	39	23
Stratum 7				
Different backwaters sampled	16	17	14	14
Total nets set	53	41	42	35
CS captures	23	23	21	18
Backwaters with CS captures	8	5	6	7
Highest captures from one BA	9	8	11	7

Table 3. Number of sample backwaters per kilometer, capture backwaters per sample backwater, number of Colorado squawfish captures per net set, and number of captures at highest capture site divided by total captures.

	Year				
	1991	1992	1993	1994	Mean
Backwaters/km					
Stratum 1	0.29	0.19	0.29	0.42	0.30
Stratum 2	N/A	0.14	0.11	N/A	0.12
Stratum 3	0.25	0.17	0.30	0.17	0.22
Stratum 5	0.45	0.27	0.25	0.25	0.30
Stratum 6	0.78	0.98	0.88	0.91	0.89
Stratum 7	0.70	0.75	0.62	0.62	0.67
Capture BA/total BA					
Stratum 1	0.16	0.23	0.45	0.31	0.29
Stratum 2	N/A	0.50	0.33	-	0.42
Stratum 3	0.30	0.29	0.42	0.22	0.31
Stratum 5	0.25	0.08	0.18	0.18	0.24
Stratum 6	0.30	0.34	0.31	0.26	0.30
Stratum 7	0.50	0.29	0.43	0.50	0.43
Captures/net set					
Stratum 1	0.92	0.42	0.47	0.40	0.55
Stratum 2	N/A	0.67	0.29	-	0.48
Stratum 3	0.30	0.75	0.51	1.00	0.64
Stratum 5	0.31	0.13	0.21	0.12	0.19
Stratum 6	0.27	0.55	0.96	0.95	0.68
Stratum 7	0.43	0.56	0.50	0.51	0.50
Highest number captured at one site/total captured					
Stratum 1	0.55	0.46	0.26	0.28	0.39
Stratum 2	N/A	0.75	1.00	-	0.89
Stratum 3	0.33	0.78	0.37	0.89	0.59
Stratum 5	0.46	1.00	0.75	0.50	0.68
Stratum 6	0.42	0.37	0.78	0.58	0.54
Stratum 7	0.39	0.35	0.52	0.39	0.41

Movements

Fish Tagged in the Upper Reach

Of those Colorado squawfish initially captured and tagged in the upper reach, 69 were subsequently recaptured at least once, and some were recaptured two or more times. Seven recaptured fish were initially tagged in 1990; 21 in 1991, 23 in 1992, 13 in 1993; five in 1994. Including multiple captures of the same fish, there was a total of 92 recaptures during 1991-1995. Of these, only 15 (16.3%) were located > 10 km from the previous capture site. Twelve of the 15 (80%) were upstream displacements (Fig. 3); two were downstream; one was both downstream and upstream (the fish traveled down the Colorado River before moving up the Gunnison River where it was recaptured). Percent displacements upstream was significantly higher ($P = 0.0433$) than one would predict if direction of movement was random (50% upstream). None of the fish located in the upper reach during the study period were later recaptured in the lower reach.

Fish Tagged in the Lower Reach

Thirty-seven different Colorado squawfish initially captured in the lower reach were subsequently recaptured one or more times, providing a total of 43 recaptures during 1992-1995. This included seven initially tagged in 1991; 20 in 1992; seven in 1993; three in 1994. This included three individuals captured in October. Though outside the spring study period, these were included because the capture-recapture intervals were > 1 yr and October is well beyond the pre- and post-spawning migration period. Two of these fish were initially captured during October 1991 in the Colorado River by UDWR, and were 14.8 and 16.1 km downstream of the lower end of the study area; they were included because they later moved into the study area. Twenty-five of the 43 recaptures (58%) were located > 10 km from the previous capture site. Seventeen (68%) of these displacements were directed upstream (Fig. 4). However, unlike for upper-reach fish, no extensive search was conducted for lower-reach fish downstream of the lower end of the lower-reach study area. Hence, if tagged fish moved downstream and out of the study area, there could have been a greater percentage of fish that moved in a downstream direction than our data indicate. However, this source of error was probably low given that UDWR and other researchers working downstream of our study area during this period did not recapture any of our tagged fish. The percentage of fish moving > 10 km in an upstream direction was not significantly higher than 50% ($P = 0.0863$). However, when those moving > 25 km were examined, the percent having moved upstream (74%; N = 23) was significantly higher than 50% ($P = 0.018$).

Unlike upper-reach fish, many lower-reach-tagged fish moved into the adjoining reach: over the 5-year period, 11 of 25 movements > 10 km (44%) were from the lower reach to the upper reach. During 1992, there was only one recapture of a fish initially tagged in the lower reach; it was recaptured in the lower reach. During 1993, there were 14 lower-reach-tagged fish recaptured; two (14%) of these were in the upper reach. During 1994, the last year of systematic, river-wide surveys, there were 16 lower-reach-tagged fish recaptured; of these, five (31%) were in the upper reach. In 1995, searches did not cover the entire river, but large

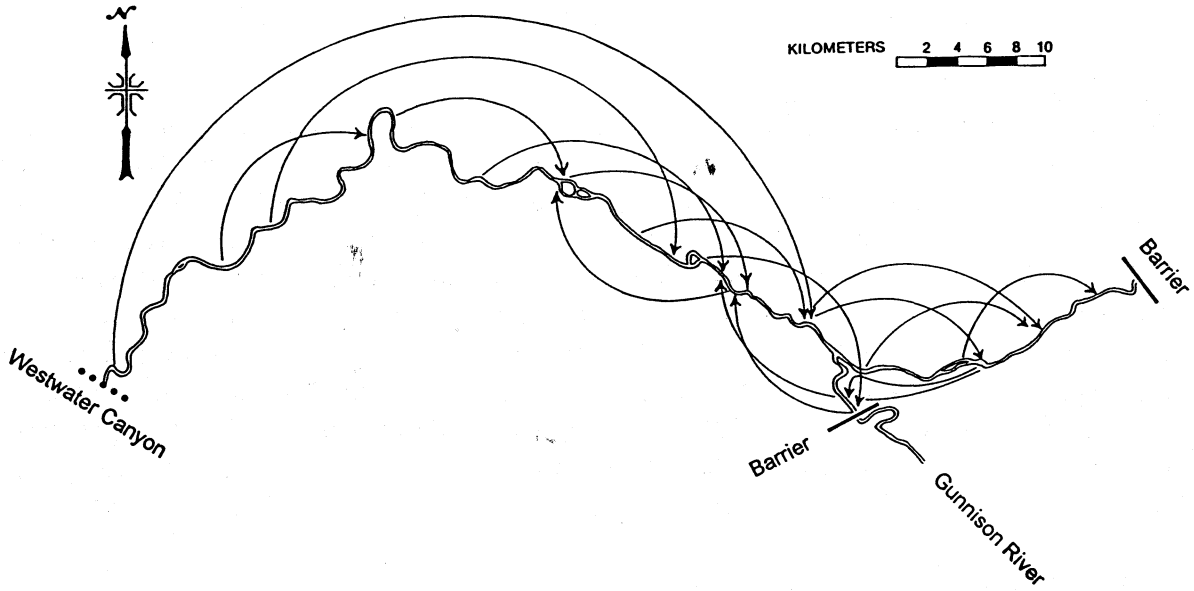


Figure 3. Movement of Colorado squawfish PIT-tagged in the upper-reach study area. Origin of arrows represent capture location and points of arrows represent location of next capture. Only movements > 10 km are shown. Consecutive captures are one or more years apart. Arrows above the river signify upstream movement; arrows below the river signify downstream movements.

sections of each reach were sampled. Of 12 recaptured fish initially tagged in the lower reach, five (42%) were in the upper reach. Because search effort was not constant between reaches in any year, percentages of lower-reach-tagged fish later found in the upper reach are probably not reflective of true proportions of fish moving from or remaining in the lower reach in any year, i.e., if search effort was greater in one reach, there would be a greater likelihood of capturing previously tagged fish there than in the less-searched reach. However, the data are useful to the extent that a trend is indicated: the proportion of fish initially captured in the lower reach that later moved to the upper reach continued to increase with the passage of time.

Size Effects on Extent of Movement

Distance moved between captures was inversely related to fish size; i.e., distance moved decreased with increased fish size. Mean distance between capture sites of Colorado squawfish < 500 mm TL (at time of second capture) was 43.8 km (SE = 15.5; N = 17). For Colorado squawfish 500-599 mm TL (between first and second captures), mean displacement between consecutive captures was 13.3 km (SE = 3.5; N= 68). For Colorado squawfish ≥ 600 mm (at first capture), mean displacement between captures was 3.1 km (SE = 0.8; N = 34). Mean displacement of fish 500-599 mm TL and fish ≥ 600 mm TL was not statistically different, but mean displacement of both groups was less than that of fish < 500 mm TL

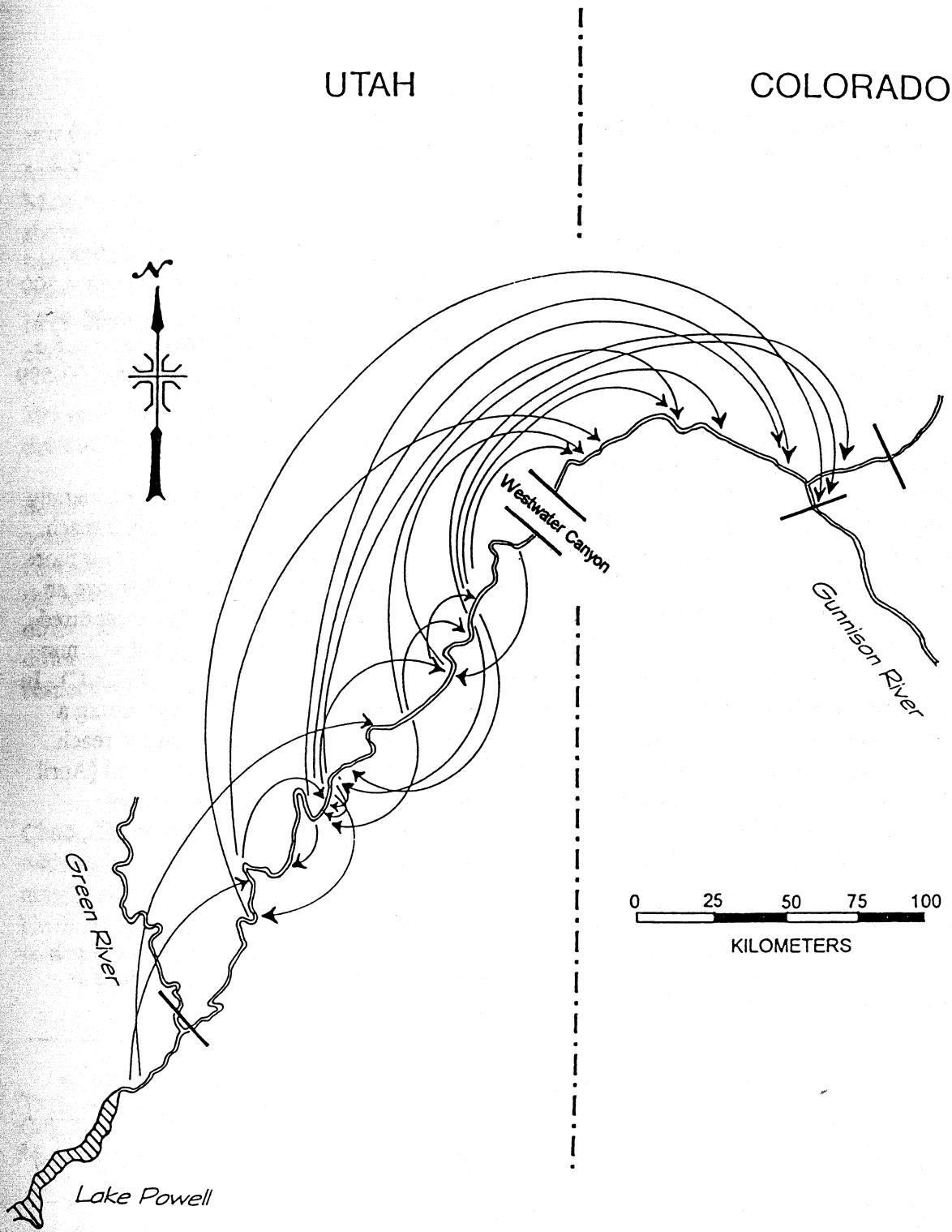


Figure 4. Movement of Colorado squawfish PIT-tagged in the lower reach study area. Origin of arrows represent capture location; points of arrows represent location of next capture. Only movements > 10 km are shown. Consecutive captures are one or more years apart. Arrows above the river signify upstream movement; arrows below the river signify downstream movements.

($P < 0.05$). Additionally, displacement of fish ≥ 550 mm TL (7.5 km; SE = 2.5; N = 70) was also significantly less ($P < 0.0082$; T-test) than for fish < 550 mm TL (33.6 km; SE = 10.2; N = 30).

Only 6% of capture-recapture displacements were > 10 km for fish > 600 mm TL at first capture. For fish 500-599 mm TL, 28% of displacements were > 10 km; for those fish < 500 mm TL, 59% of displacements were > 10 km. These differences in percentages among size classes were significant: percent displacements > 10 km for fish ≥ 600 mm was less than for fish 500-599 mm ($P = 0.009$) and for fish < 500 mm ($P = 0.00007$); percents for fish 500-599 mm were also less than for fish < 500 mm ($P = 0.003$).

Size of Fish Moving to the Upper Reach

Also of interest is whether there might be a minimum size that Colorado squawfish generally attain before they are capable or sufficiently motivated to move to the upper reach, a reach inhabited primarily by adults. Unfortunately, in many instances recaptures were two or more years from previous captures, which made it difficult to determine when, or at what size an individual made its move. Only six individuals recaptured in the upper reach were captured the previous year in the lower reach (Table 4). The smallest was between 421 and 449 mm TL (Fish No. 186) when it moved; the largest was between 555 and 577 mm TL (Fish C). In addition to these fish, there were others that moved to the upper reach sometime during a multi-year period. None were smaller than 449 mm TL when captured in the upper reach. One fish (No. 467) that moved to the upper reach sometime during a 2.5-year period (April 1992 - October 1994) was between 570 and 628 mm TL. Thus, the smallest fish we documented moving from the lower to the upper reach was no larger than 449 mm TL, and the largest fish was at least 570 mm TL.

Table 4. Lengths of Colorado squawfish before and after movement from the lower reach to the upper reach. Only those fish moving between reaches based on capture-recapture in consecutive years are included.

	Lower reach capture			Upper reach capture		
Fish No.	Year	RK	length(mm)	Year	RK	length(mm)
129	92	81.5	438	93	175.2	478
131	94	96.2	535	95	132.0	580
186	92	98.9	421	93	154.3	449
238	93	58.2	523	94	147.1	539
323	93	26.5	456	94	GU-1.1	466
C	94	97.6	555	95	147.5	577

Body Condition

Mean body condition of Colorado squawfish varied with river reach and fish size class. Month-specific constants from the mass-length relationships used in calculating condition are shown in Table 5. In the lower reach, fish condition declined with increasing size (Fig. 5). Mean *Kn* of fish of both 500-599 and 600-699 mm TL length classes were lower ($P < 0.05$) than for fish of three smaller length classes: 200-299 mm, 300-399 mm and 400-499 mm TL. In contrast, condition of upper-reach fish increased with increasing fish size; maximum condition was reached in fish 700-799 mm TL. Mean *Kn* of fish 600-699 mm TL was higher ($P < 0.05$) than that of fish 400-499 mm and of fish 500-599 mm TL. Mean *Kn* of fish 700-799 mm was higher than that of fish 600-699 mm TL ($P < 0.05$). No difference was detected between fish 800-899 mm long and other 100-mm length groups.

Mean *Kn* began to differ between reaches once fish attained ≈ 500 mm TL. However, reach comparisons could not be made for all length classes because no fish 200-299 mm TL were captured in the upper reach and only two 300-399-mm-TL-class fish were captured there. In the lower reach, no fish 700-799 or 800-899 mm TL were captured. Though we detected no difference in mean *Kn* between upper and lower reach fish 400-499 mm TL, mean *Kn* was different between reaches for fish 500-599 and 600-699 mm TL ($P = 0.0023$ and $P = 0.0037$, respectively).

Relative Abundance of Forage Fish

Catch rates of native fish were generally higher in the upper reach than in the lower reach, with highest catch rates occurring in the uppermost strata. Native fish susceptible to trammel netting and electrofishing were the larger species; besides Colorado squawfish, these included bluehead sucker, flannelmouth sucker and roundtail chub. Smaller native fish (< 70 mm TL) present, but not included in the analysis, were speckled dace (*Rhinichthys osculus*).

Table 5. Mass-length regression coefficients of Colorado squawfish captured from the Colorado River during 1990-1994. $Log_{10}M_e$ = ((Log_{10} length) slope) + y-intercept, where M_e is the expected mass in grams.

Month	n	Slope	(SE)	y-intercept	(SE)	R^2
April	81	3.17326	(0.061)	-5.54824	(0.167)	0.972
May	257	3.25981	(0.030)	-5.77281	(0.083)	0.978
June	128	3.20661	(0.038)	-5.60323	(0.010)	0.983

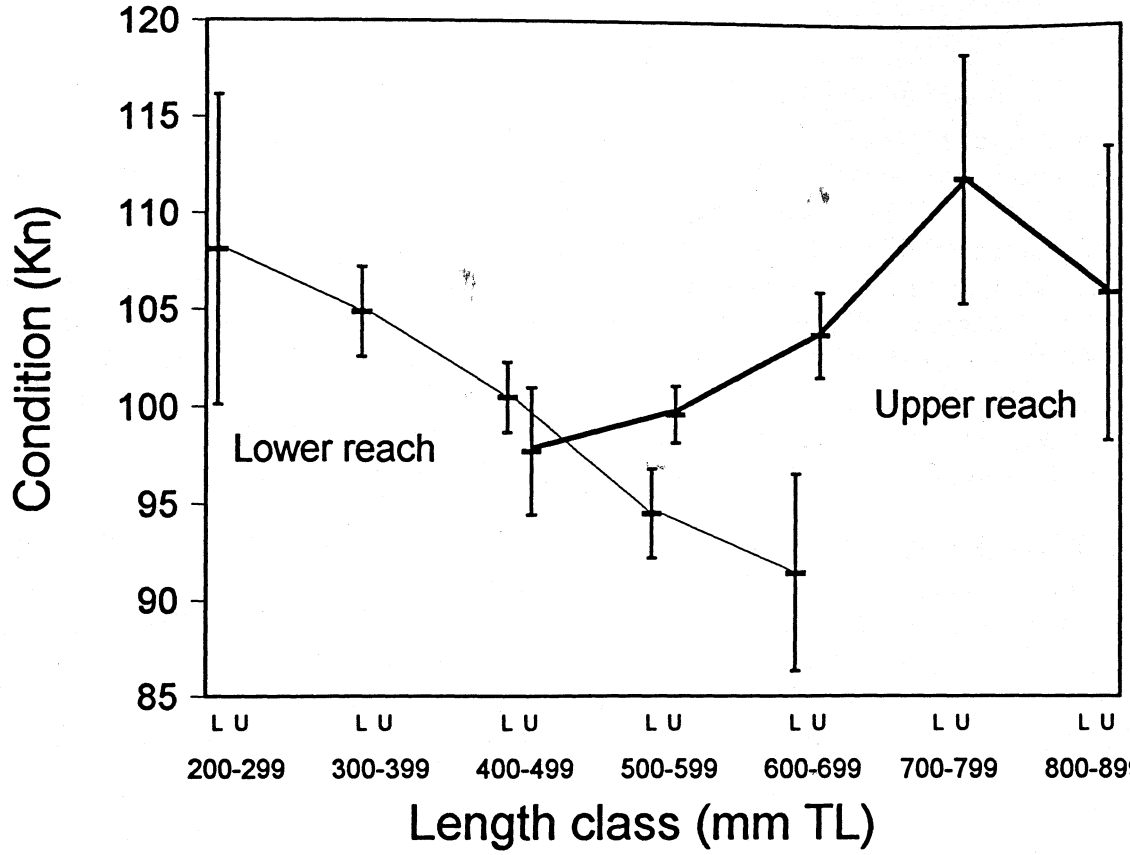


Figure 5. Mean relative condition (*Kn*) of Colorado squawfish by length class and reach. Error bars represent 95% confidence intervals. L = lower reach; U = upper reach.

Nonnative species susceptible to the two gear types included common carp, channel catfish and white sucker. There were also incidental catches of other non-native species that we considered unimportant for this analysis.

In the lower reach, electrofishing catch rates of native fish were higher in Stratum 3 than in Stratum 1 ($P > 0.05$), though other among-strata differences were not significant. Catch rates in upper-reach strata 5-7 were all higher ($P < 0.05$) than in lower-reach strata (Fig. 6). Among upper-reach strata, catch rate in Stratum 7 was higher than in strata 5 and 6 ($P > 0.05$); no difference was detected between strata 5 and 6.

Trammel-netting catch rates of native fish displayed a similar trend to those of electrofishing, with rates generally increasing upstream. Variation among years was not significant within any one stratum. No sampling was done in Stratum 2 during 1994. Differences among lower-reach strata were not significant ($P > 0.05$) during any year. CPUE in Stratum 5 was higher ($P < 0.05$) than in Stratum 1 during 1992 and 1994, though not in 1993; it was higher than in Stratum 3 only in 1994. Stratum 6 CPUE was significantly higher than CPUE in

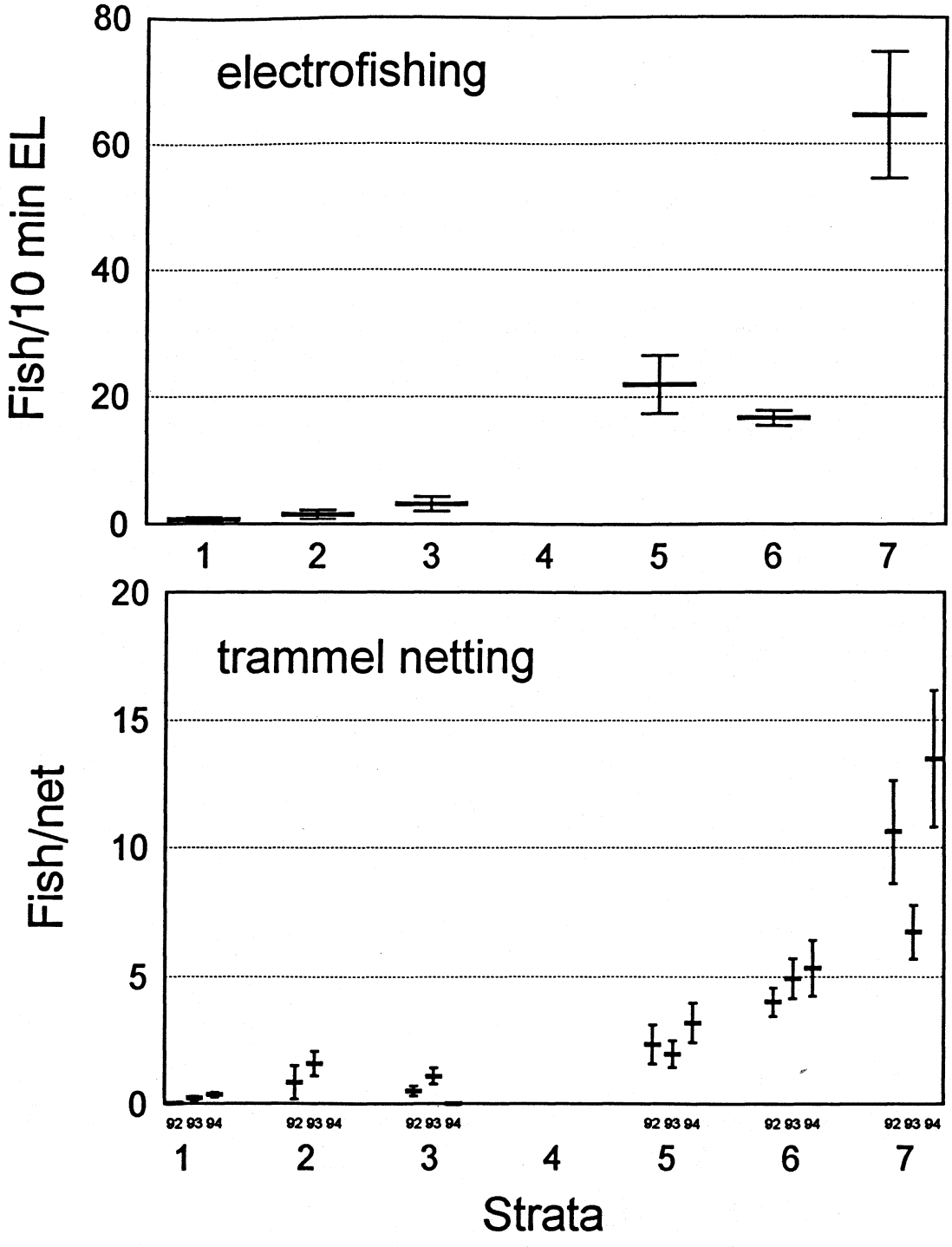


Figure 6. Electrofishing (top) and trammel-netting (bottom) total catch-per-unit-effort by stratum for roundtail chub, flannelmouth sucker and bluehead sucker combined. Trammel netting was conducted in 1992, 1993, and 1994; electrofishing was conducted in 1993 only. Bars represent the mean +/- 1 SE.

Stratum 1 during all years; higher than in strata 3 and 5 in 1993 and higher than in Stratum 3 in 1994. Stratum 7 CPUE was higher than all other strata during all years, except in 1993 when the difference between strata 6 and 7 was not significant. When data from the three years were pooled, Stratum 6 CPUE was higher than in Stratum 5, and Stratum 7 CPUE was higher than in all other strata.

White suckers were relatively rare except in Stratum 7 where mean CPUE was 0.6-1.0 fish/net, depending on the year. Mean CPUE for white suckers in strata downstream of Stratum 7 was always < 0.2 fish/net.

For channel catfish and common carp, no differences in electrofishing catch rates were detected among strata. However, when catch of the two species were pooled, catch rate in Stratum 6 was significantly higher ($P < 0.05$) than in strata 1 and 7. For trammel netting, no CPUE differences were detected among years within strata and differences among strata were few.

For fish < 300 mm TL, mean electrofishing CPUE was higher in all three upper reach strata than in lower reach strata (Fig. 7). The ANOVA was significant ($P < 0.0000001$) and multiple comparisons indicated that rates in strata 1, 2 and 3 were all different from rates in strata 5, 6 and 7 ($P < 0.05$). No differences were found in rates among strata 1, 2 and 3, nor among strata 5, 6 and 7.

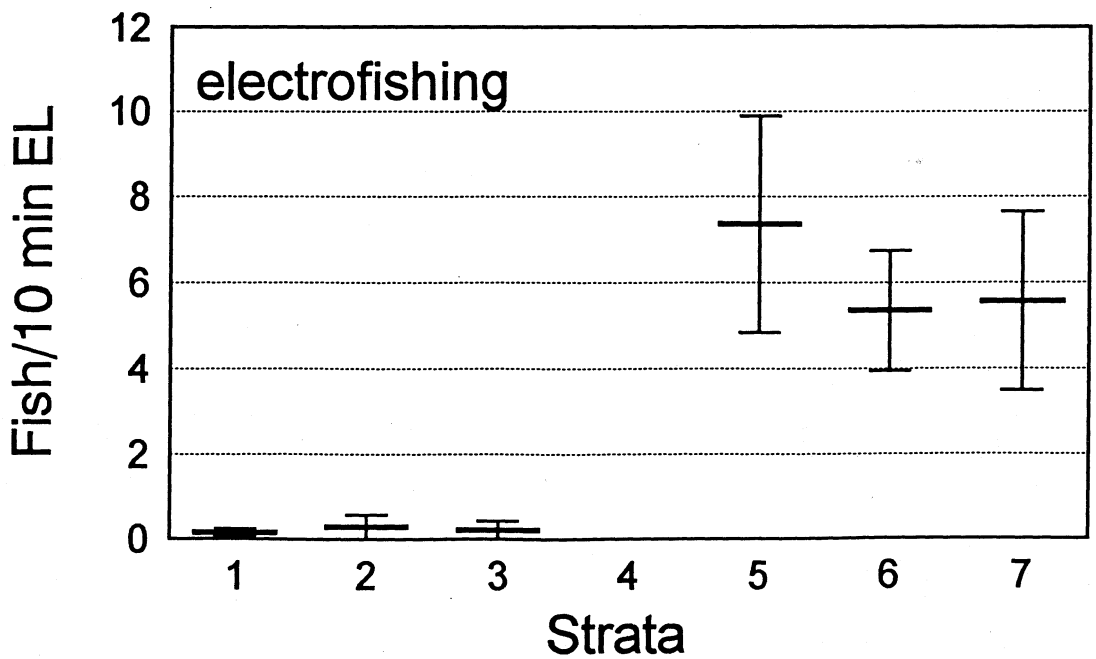


Figure 7. Electrofishing total catch-per-unit-effort by stratum for fish < 300 mm TL. All species except channel catfish are included. Bars are the mean +/- 1 SE.

DISCUSSION

Fortuitously, our four-year study coincided with a period during which 2-3 consecutive strong year classes of Colorado squawfish, hatched in the mid-1980's, were recruiting to the adult population (see Osmundson and Burnham 1996). This not only allowed us to monitor the movements of many individual fish, it also allowed us to document the impact a strong year class can have on adult distribution. Colorado squawfish in the Colorado River were not uniformly distributed. Distribution was stratified by fish size which increased in an upstream direction. This size stratification was most pronounced early in the study. As the study progressed, recruitment to the adult population strongly influenced average sizes of fish throughout the river. Mean lengths in lower-reach strata increased as these young fish grew and there was an infusion of young adults to upper reach strata which lowered average sizes of fish there.

In addition to changes in average size, recruitment and dispersal of the mid-1980's year classes also affected adult numbers in various strata. Our only index to relative densities of adults was trammel-netting catch rate. Initially, very few adults were found in the lower reach. Between 1991 and 1993, catch rates of adults > 500 mm TL in the lower reach increased ten-fold (0.02 to 0.20 fish/net). By 1994, catch rates leveled out at 0.20 fish per net. In the upper reach, the overall catch rate increased from 0.30 in 1991 to 0.57 in 1993 and also apparently leveled off, remaining at 0.57 in 1994. On a per-stratum basis, variation among years was difficult to discern for strata 2 and 3 where numbers of backwaters were few. In Stratum 5, deposits of silt in the mouths of many backwaters following 1991 restricted fish access and probably biased netting results. Catch rates of adults increased in Stratum 1 and Stratum 6 between 1991 and 1993 suggesting that numbers of fish in these strata were below the level that these strata could support prior to the recruitment of this pulse of new fish.

Distance moved between captures was related to fish size and reach of initial capture. However, size and reach were related. Most fish captured and recaptured in the upper reach had not moved far from initial sites. In the lower reach, where most fish were young, most recaptures occurred > 10 km from initial captures. In both reaches, the majority of movements were directed upstream. These results suggest that young fish move more than older fish and that upon arrival at the upper reach they move less. This is similar to the behavior of flannelmouth suckers in the White River noted by Chart and Bergerson (1992); where young individuals of that species also moved more than older ones.

Our results indicate that as Colorado squawfish grow and mature they tend to move upstream. This suggests that adults prefer upper reach habitats over lower reach habitats. Particularly revealing is that no fish captured in the upper reach later dispersed to the lower reach. The exception to this was one fish initially tagged in the lower Gunnison River in 1994 and

recaptured in the lower reach (km 141.9) in 1995; it was excluded from the analysis because the initial capture was during the spawning season. We suspect that older, larger fish select a home feeding range to which they maintain fidelity, as previously suggested by Wick et al. 1983, Wick and Hawkins (1989) Tyus (1990) McAda and Kaeding (1991), Irving and Modde (1994) and Ryden and Ahlm (1996). Though adults are relatively few in number, averaging 2.4 fish/km in the upper reach (Osmundson and Burnham 1996), ideal physical habitat or food resources might be limited and variable in time and space. It is unknown whether these fish are territorial; however, if the number of preferred areas are limited in a given year or reach, adults would likely distribute themselves in a way that minimizes intraspecific competition. Perhaps, as the best areas are vacated when larger fish are removed or die, they are refilled by other large fish.

Though good physical habitat and feeding areas might be found in all reaches, some reaches may have greater densities of preferred habitats. If large adults are behaviorly dominant, average size of fish may be an indication of habitat quality or the degree to which a reach is preferred over others. If so, we might speculate that Stratum 7 contains the greatest concentration of quality adult habitat in the upper Colorado River. Another possibility is that large adults have different requirements than smaller or sub- adults and habitats preferred by large adults could become filled while space for smaller adults be still available. Preference for a given reach suggests the reach contains the best habitat; however, this does not necessarily mean that such a reach has the greatest capacity to support adults on a per unit basis (i.e., fish/km). Though the differences were not significant, catch rates appeared to be higher in Stratum 6 than in Stratum 7 during 1993 and 1994. Given that the density of backwaters in Stratum 6 was higher than in Stratum 7, higher catch rates there could not be explained by fish concentrating in scarcer backwaters. We speculate that carrying capacity, in terms of number of fish a kilometer of river can support, is higher in Stratum 6 than in Stratum 7. This is not unexpected given that volume of water there is ≈1.7 times (annual average) that of Stratum 7 because of the Gunnison River inflow.

The high *Kn* values of young Colorado squawfish (200-400 mm TL) in the lower reach suggests that food availability was not limited during the spring period. Condition during the remainder of the year was not investigated. High numbers of small-bodied, non-native minnows in backwaters throughout the river (McAda et al. 1994) likely provide an abundant food source for young Colorado squawfish. However, as Colorado squawfish in the lower reach grew, their condition during spring declined. One possible explanation is that as these piscivores grow, they need a larger forage item to maintain condition. At ≈500 mm TL, a diet consisting entirely of small minnows may begin to be less than optimum for Colorado squawfish.

River-wide variation in catch rates of prey species along with reach differences in body condition suggests that a net movement of larger fish to the upper reach is a response to food resource gradients. Based on differences in body condition for similar-sized fish, a move to the upper reach was clearly rewarding for fish 500-700 mm long. Poor condition of adults

that we detected in the lower reach suggests that food resources were limiting and that adults may have exceeded their carrying capacity there. The scarcity of adults in the lower reach in 1991, prior to the recruitment of the strong, mid-1980's year classes, suggests that over time, most adults eventually leave the lower reach and become concentrated in the upper reach. If the net upstream movement of larger fish that we observed continues, intraspecific competition for scarce food resources in the lower reach may decline.

Factors that motivate adult Colorado squawfish to make significant movements are unknown, but presumably involve the three basics of life: growth, survival, and reproduction. Motivational urges arise from the need to eat, the need to avoid predation, and the need to spawn. For adult Colorado squawfish in the Colorado River, the need to avoid predation is probably the least important. To date, northern pike (*Esox lucius*), a large non-native piscivore that recently invaded the Green and Yampa river systems (Tyus and Beard 1990, Nesler 1995), is extremely rare in the Colorado River. Though very large channel catfish and large Colorado squawfish might prey on small sizes of adult Colorado squawfish, such large individuals are rare. Given that seasonal movements related to spawning were excluded from our analyses, the urge to feed and grow coupled with longitudinal variation in food availability remains the most likely explanation for the observed long-distance displacements.

Though food availability may best explain the distributional pattern of adult Colorado squawfish, seasonal timing of movements and the motivational force behind such movements could not be discerned here due to the limitations of our study design, i.e., movement was detected simply by comparing an individual's location one year with that in a previous year. Movements may be motivated by hunger, with upstream exploration for food being rewarded more than downstream exploration, resulting in a net upstream shift in adult distribution. Upstream dispersal could perhaps be an innate physiological mechanism. An alternative explanation is that movements are motivated by the urge to spawn; in the process, discovery of better feeding areas could occur by chance. Remaining in such areas rather than returning to initial locations would also result in long-distance net displacements. The fact that movement from the lower reach to the upper reach occurred only after squawfish had reached a sexually mature size (450-570 mm TL) lends some support to this hypothesis. However, large numbers of adult fish found in reaches far above spawning areas, such as in the upper White and Yampa rivers suggests that these feeding areas were not located while en route to a spawning site. In either scenario, variation in food availability would be the cause of displacement, only the mechanism of discovery differs.

Population size of adult Colorado squawfish in the Colorado River is likely limited by low frequencies of strong year classes (Osmundson and Burnham 1996). After consecutive, strong year classes recruited to the adult population during our study, netting catch rates of Colorado squawfish > 500 mm TL significantly increased in Stratum 1 of the lower reach and likely increased in Stratum 6 of the upper reach. However, in Stratum 7, a high use area for adults, catch rates evidently did not increase during this period perhaps suggesting that adult habitat was limited there. If the frequency of strong year classes can be increased through

management efforts, the next factor likely limiting population increase could be adult carrying capacity, i.e., suitable physical habitat or food availability. How many adults the river can currently support is unknown. Low condition factors exhibited by adults in the lower reach suggest that fish exceeded their food supply during our study period. Methods for increasing the number of adults the river can support in good condition include improving existing habitat through flow management (see Osmundson et al. 1995) and providing access to historically used reaches now vacant or underutilized due to instream barriers. In the upper Colorado River, two such areas may be available: the Gunnison River upstream of the newly constructed Redlands fish ladder and the Colorado River upstream of the Price Stub and Government Highline dams. As this study demonstrates, Colorado squawfish are very capable of distributing themselves if levels of reproduction and recruitment can be improved.

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Appendix Table I. Displacement of Colorado squawfish initially captured and marked in the upper reach study area. Only those fish subsequently recaptured are shown. Displacement distances are shown in miles and kilometers; river locations are in miles. Captures that occurred outside the seasonal study period and therefore were not used in the analyses are indicated (NA).

AGENCIES	FISH NO.	SIZE	Distance mi	Distance km	DIRECTION	YEAR CAPTURED 90	91	92	93	94	95
MARKED IN UPPER RIVER											
FW-FW	3	589-603	1.2	1.9	DOWN	164.8			163.6		
FW-FW	15	610-730	3.6	5.8	DOWN	179.1				175.5	
FW-FW	17	593-624	8.1	13.0	UP	175.2	183.1	181.8		175.7	
FW-FW	17	624-645	1.5	2.4	DOWN						
FW-FW	17	645-661	6.1	9.8	DOWN						
FW-FW	18	540-570	0.0	0.0	NONE	163.8			163.8	163.5	163.6-NA
FW-FW	18	570-574	0.3	0.5	DOWN						
FW-FW	18	574-591	0.1	0.2	UP-NA						
FW-FW	19	573-582	0.0	0.0	NONE	163.7		163.7	163.6		163.4
FW-FW	19	582-583	0.1	0.2	DOWN						
FW-FW	19	583-586	0.2	0.3	DOWN						
FW-FW	20	575-670	9.2	14.8	UP	158.6				167.8	
FW-FW	21	539-548	0.2	0.3	UP	179.1	179.3	179.5			
FW-FW	21	548-560	0.2	0.3	UP						
FW-FW	24	572-582	8.2	13.2	UP		167.8		176.0		
FW-FW	25	775-807	4.5	7.2	UP		167.8				2.1
FW-FW	27	628-650	0.0	0.0	NONE		167.8			167.8	
FW-FW	28	590-649	4.0	6.4	UP-NA		164.9			168.9-NA	
FW-FW	29	612-659	4.3	6.9	DOWN		167.8				163.5
FW-FW	30	754-777	1.0	1.6	UP		162.8		163.8		
FW-FW	31	560-568	0.0	0.0	NONE		176.7	176.7			
FW-FW	34	672-675	0.6	1.0	UP		175.2	175.8	175.3		
FW-FW	34	675-678	0.5	0.8	DOWN						
FW-FW	35	582-587	0.1	0.2	UP		175.2	175.3			
FW-FW	38	582-597	8.4	13.5	UP		171.6		180.0		
FW-FW	42	853-856	2.4	3.9	UP		134.4		136.6		
FW-CO	43	552-580	0.1	0.2	UP		134.2				134.3
CO-CO	45	448-483	17.5	28.2	UP-NA		144.8	162.3-NA			
FW-FW	46	567-636	2.8	4.5	UP		179.8			182.6	
FW-FW	47	556-564	0.4	0.6	UP		179.1	179.5			
FW-FW	51	630-632	0.1	0.2	UP		175.8	175.9		175.8	
FW-FW	51	632-639	0.1	0.2	DOWN						
FW-FW	55	505-520	10.3	16.6	UP		144.2	154.5			
FW-FW	59	537-551	1.3	2.1	DOWN		181.8		182.0		
FW-FW	60	698-768	13.3	21.4	DOWN		176.6				163.3
FW-FW	62	664-676	6.4	10.3	DOWN-NA		175.3			168.9-NA	
FW-FW	63	566-573	0.1	0.2	DOWN		175.3		175.2		
FW-CO	64	424-467	7.8	12.6	UP		134.2		142.0		
FW-FW	66	581-597	0.3	0.5	DOWN		1.4		1.1		
FW-FW	69	628-633	0.0	0.0	NONE-NA		176.6			176.6-NA	
FW-FW	86	502-530	0.1	0.2	UP		163.6	163.7		3-NA	
FW-FW	86	530-571	9.5	15.3	UP-NA						
FW-FW	87	865-880	0.3	0.5	UP-NA		158.6			158.9-NA	
FW-FW	110	758-801	0.9	1.4	DOWN-NA		175.3-NA			174.4	
FW-FW	111	676-686	9.5	15.3	DOWN-NA		3.0-NA	163.7			
FW-FW	112	772-801	4.3	6.9	DOWN-NA		3.0-NA			168.9-NA	2.0
FW-FW	112	801-804	3.3	5.3	UP-NA						
CO-FW	116	544-549	32.7	52.6	UP-NA		135.5-NA	168.2			
FW-FW	118	580-597	1.7	2.7	UP			1.3	3.0		2.8-NA
FW-FW	118	597-622	0.2	0.3	DOWN-NA						
FW-FW	119	563-568	0.3	0.5	UP			168.2	168.6	168.7	
FW-FW	119	568-587	0.1	0.2	UP						
FW-FW	120	600-610	4.5	7.2	DOWN			168.3	163.8	163.5	163.3
FW-FW	120	610-615	0.3	0.5	DOWN						
FW-FW	120	615-616	0.2	0.3	DOWN						
FW-FW	121	547-554	12.2	19.6	UP			167.8	180.0		
FW-FW	122	575-588	9.3	15.0	UP-NA			163.9		3.0-NA	
FW-FW	123	533-597	0.5	0.8	DOWN			163.9			163.4

Appendix Table I continued.

AGENCIES	FISH NO.	SIZE	Distance mi	Distance km	DIRECTION	YEAR CAPTURED 90	91	92	93	94	95
					MARKED IN UPPER RIVER (CONT.)						
FW-FW	125	712-764	9.5	15.3	DOWN			3.0			163.7
FW-FW	141	654-674	1.8	2.9	DOWN			181.8	180.0		
FW-FW	142	665-696	1.2	1.9	DOWN			176.7		175.5	
FW-FW	143	613-616	0.2	0.3	DOWN			175.9		175.7	
FW-FW	145	645-708	5.0	8.0	DOWN-UP			175.3			1.5
FW-FW	147	568-573	0.0	0.0	NONE			170.9	170.9		
FW-FW	150	535-568	0.7	1.1	UP-NA			168.2		168.9-NA	
FW-FW	158	472-482	0.2	0.3	DOWN			164.0	163.8	169.6-NA	163.4
FW-FW	158	482-498	5.8	9.3	UP-NA						
FW-FW	158	498-503	0.4	0.6	DOWN						
FW-CO	159	545-586	0.1	0.2	UP			163.7	163.8	163.5	163.6-NA
CO-FW	159	586-590	0.3	0.5	DOWN						
FW-FW	159	590-619	0.1	0.2	UP-NA						
FW-FW	160	539-550	1.1	1.8	UP			162.7	163.8		
FW-FW	161	564-577	1.1	1.8	UP			162.7	163.8	168.7	
FW-FW	161	577-580	4.9	7.9	UP						
FW-FW	169	560-582	43.3	69.7	UP			124.9	168.2		
CO-CO	172	425-488	3.9	6.3	DOWN			151.3		147.4	
FW-FW	173	560-573	0.1	0.2	UP			163.7	163.8	163.5	163.4
FW-FW	173	573-573	0.3	0.5	DOWN						
FW-FW	173	573-577	0.1	0.2	DOWN						
FW-FW	174	502-514	0.1	0.2	DOWN			163.7	163.6	163.5	165.5
FW-FW	174	514-518	0.1	0.2	DOWN						
FW-FW	174	518-534	0.0	0.0	NONE						
FW-FW	175	628-632	0.2	0.3	DOWN			163.7	163.5		
FW-FW	178	700-736	0.2	0.3	DOWN			163.7			163.5
FW-FW	179	524-553	12.0	19.3	UP			161.2		3.0	
FW-FW	180	528-564	10.3	16.6	UP-NA			158.6		168.9-NA	
FW-FW	199	652-722	0.0	0.0	NONE-NA			2.8-NA			2.8-NA
FW-FW	200	498-512	33.6	54.1	UP-NA			130.2-NA	163.8		163.5
FW-FW	200	512-535	0.3	0.5	DOWN						
FW-FW	203	615-631	0.1	0.2	DOWN				163.7		163.6
FW-FW	204	582-588	0.2	0.3	DOWN				163.7	163.5	163.4
FW-FW	204	588-598	0.1	0.2	DOWN						
FW-FW	210	555-558	0.4	0.6	DOWN				168.2	167.8	
FW-FW	214	875-881	20.3	32.7	DOWN-NA				150.5	130.2-NA	163.3
FW-FW	214	881-889	12.8	20.6	UP						
FW-FW	216	525-569	24.3	39.1	UP				135.2		159.5
FW-FW	217	565-591	6.9	11.1	DOWN-UP				176.0		2.7
FW-FW	218	601-631	0.1	0.2	DOWN				163.6	163.5	
CO-CO	262	614-662	2.2	3.5	UP				132.1		134.3
FW-FW	290	597-607	0.3	0.5	DOWN				163.8	163.5	163.5
FW-FW	290	607-610	0.0	0.0	NONE						
FW-FW	291	508-546	0.3	0.5	DOWN				163.8		163.5
FW-FW	292	578-594	4.8	7.7	UP				158.7		163.5
FW-FW	310	471-489	9.5	15.3	DOWN				163.8	154.3	163.8
FW-FW	310	489-523	9.5	15.3	UP						
FW-FW	311	580-584	0.3	0.5	DOWN				163.8	163.5	163.4
FW-FW	311	584-592	0.1	0.2	DOWN						
FW-FW	314	474-510	4.8	7.7	DOWN				175.3	170.5	
FW-FW	397	508-572	0.7	1.1	DOWN-NA					164.0	163.3-NA
FW-FW	400	511-532	0.0	0.0	NONE					163.5	163.5
FW-FW	403	652-673	0.0	0.0	NONE					163.5	163.5
FW-FW	404	682-696	0.0	0.0	NONE					163.5	163.5
FW-FW	405	509-563	0.0	0.0	NONE					163.5	163.5
FW-FW	406	549-568	0.2	0.3	DOWN					163.5	163.3
FW-FW	426	856-860	4.6	7.4	UP-NA					168.3-NA	2.7-NA
FW-FW	462	809-809	1.0	1.6	UP-NA					2.0-NA	3.0-NA
FW-UT	452	554-565	85.0	136.8	DOWN-NA					3.0-NA	88.2

Appendix Table II. Displacement of Colorado squawfish initially captured and marked in the lower reach study area. Only those fish subsequently recaptured are shown. Displacement distances are shown in miles and kilometers; river locations are in miles. Captures that occurred outside the seasonal study period and therefore were not used in the analyses are indicated (NA).

AGENCIES	FISH NO.	SIZE	Distance mi	Distance km	DIRECTION	YEAR CAPTURED 90	91	92	93	94	95
					MARKED IN LOWER RIVER						
FW-FW	76	374-496	0.0	0.0	NONE		58.2		58.2		
FW-FW	79	401-518	0.0	0.0	NONE		58.2		58.2	3.0-NA	
FW-FW	79	518-553	115.0	185.0	UP-NA						
FW-FW	84	344-514	105.3	169.4	UP		58.2			163.5	
FW-FW	85	461-512	12.7	20.4	DOWN		58.2	45.5			
UT-FW	239	348-441	0.1	0.2	DOWN		58.3		58.2	58.2	
FW-FW	239	441-484	0.0	0.0	NONE						
UT-FW	320	356-454	43.7	70.3	UP		206.5		33.7		
UT-FW	A	375-578	130.8	210.5	UP		207.3				76.5
FW-FW	126	639-651	0.4	0.6	UP			99.8		100.2	
FW-FW	127	573-592	0.4	0.6	UP			99.8		100.2	
FW-FW	129	438-478	93.7	150.8	UP			81.5	175.2	175.3	
FW-FW	129	478-501	0.1	0.2	UP						
FW-UT	131	432-535	14.9	24.0	UP			81.3		96.2	132.0
UT-CO	131	535-580	35.8	57.6	UP						
FW-FW	138	402-540	105.3	169.4	UP			58.2			163.5
FW-FW	156	330-519	104.1	167.5	UP			34.8			138.9
FW-FW	183	422-469	32.6	52.5	DOWN			99.8	67.2		
FW-FW	184	620-624	0.4	0.6	UP			99.8	100.2	100.2	
FW-FW	184	624-624	0.0	0.0	NONE						
FW-FW	185	517-577	0.4	0.6	UP			99.8		100.2	
FW-FW	186	421-449	55.4	89.1	UP			98.9	154.3		
FW-UT	133	411-452	6.5	10.5	DOWN			63.8	57.3		
FW-UT	151	430-515	14.7	23.7	UP			34.8		49.5	
FW-UT	197	433-525	0.8	1.3	UP			58.3			59.1
UT-FW	226	555-570	34.1	54.9	DOWN			98.0	63.9		
UT-FW	249	450-509	8.6	13.8	UP			91.6	100.2		
UT-FW	295	470-499	5.4	8.7	UP			94.8	100.2		
UT-FW	241	460-515	6.4	10.3	DOWN			64.6	58.2		
UT-FW	323	375-456	35.8	57.6	DOWN			62.3	26.5	1.1	
UT-FW	323	456-466	144.8	233.0	UP						
UT-FW	B	406-563	112.4	180.9	UP-NA			51.0			163.4-NA
UT-FW	467	570-628	76.7	123.4	UP			96.3		2.8	
UT-FW	429	493-536	57.2	92.0	UP-NA			52.6		109.8-NA	53.1
FW-UT	429	536-542	0.5	0.8	UP						
FW-FW	231	488-527	0.1	0.2	DOWN				63.9	63.8	
FW-FW	237	506-532	30.4	48.9	UP				58.2	88.6	
FW-FW	238	523-539	88.9	143.0	UP				58.2	147.1	
FW-FW	240	506-548	114.8	184.7	UP-NA				58.2	2.8-NA	
FW-FW	276	345-413	19.4	31.2	UP-NA				38.8	58.2-NA	
FW-FW	280	450-518	10.0	16.1	DOWN-NA				26.5	16.5-NA	
FW-CO	297	489-575	40.4	65.0	UP				91.6		132.0
FW-FW	304	505-554	109.3	175.9	UP-NA				63.9	3.0-NA	
FW-FW	325	533-568	2.0	3.2	UP				21.7	23.7	
FW-UT	293	436-495	21.6	34.8	DOWN				112.3		90.7
UT-FW	431	481-509	44.5	71.6	UP-NA				64.9	109.4-NA	
UT-FW	364	442-494	1.8	2.9	DOWN				60.0	58.2	57.0
FW-UT	364	494-515	1.2	1.9	DOWN						
FW-UT	361	505-514	0.5	0.8	UP					58.5	59.0
FW-UT	353	523-550	24.5	39.4	DOWN					82.8	58.3
UT-CO	C	555-577	49.9	80.3	UP					97.6	147.5

STATUS AND TRENDS OF THE COLORADO SQUAWFISH IN THE UPPER COLORADO RIVER

FINAL REPORT

November
1996

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EXECUTIVE SUMMARY

Colorado squawfish (*Ptychocheilus lucius*), a large, piscivorous cyprinid formerly abundant throughout warm-water reaches of the Colorado River basin, is today restricted to upper basin reaches and has been classified an endangered species. In the upper basin, the species persists in three major river systems, the Green, the Colorado and the San Juan. Our objective was to determine the status and trend of the Colorado River population. To determine status, we estimated the size of the subadult and adult population. To determine short term trends, we examined the extent and frequency of reproduction and recruitment by monitoring larval and young-of-the- year catch rates and looked for significant changes in age or size structure of the population over the past 20 years. Past long-term trends could not be quantified because of a lack of historical data. However, we discuss our current estimates of population size in relation to historical accounts that serve as clues to former abundance. The likelihood of persistence of this population in the future is also discussed in the context of what the data suggest are limiting factors and the trends in habitat alteration and recovery activities.

We trammel netted backwaters during spring runoff each year from 1991 through 1994 to capture and mark subadult and adult Colorado squawfish. The entire range of the Colorado River population upstream of the Green River confluence was systematically sampled each year, with three complete sampling passes made annually through the upper reach (upstream of Westwater Canyon) and two annual sampling passes made through the lower reach (downstream of Westwater Canyon). Sampling effort was augmented with electrofishing in some segments where backwaters were few.

Our capture-recapture data from the multiple passes through the upper-reach study area were used for estimating, and making inferences about, survival rates, abundance, and recruitment based on open capture-recapture models. 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 within years to estimate population abundance. We also examined our trammel-netting capture rates as an additional means to detect changes in adult abundance over the four-year study period.

Size frequency analysis from lengths of captured fish allowed us to assess trends in the age structure of the population both among reaches and among time periods. Our upper-reach size-structure data were compared with those from earlier periods when years or groups of years had a sufficiently large number of capture records (> 30 length measurements from one subreach); these earlier time periods included 1974-1976, 1979, and 1982. Also, our size frequency data from the lower reach, coupled with age information from scale analyses, allowed us to determine the frequency of strong year classes during recent times.

Reproductive success in the upper reach over a nine-year period (1986-1994) was evaluated by systematically sampling for Colorado squawfish larvae with hand seines and young-of-the-year (YOY) with beach seines each summer and fall, respectively. Summary data from the Interagency Standardized Monitoring Program (McAda et al. 1994) was also examined to compare our upper reach data with lower reach YOY capture rates.

Annual survival rate for adult Colorado squawfish in the upper reach was estimated to be 0.86 (95% C.I. = 0.66-0.95). This point estimate was consistent with the point estimate calculated by Osmundson et al. (1996) using an entirely different method. Size of the adult subpopulation in the upper reach, averaged over the four-year study period, was estimated to be 263 individuals (95% C. I. = 161-440) using program CAPTURE; using program RECAP, the estimate was 253 (95% C. I. = 186-333). These census numbers equate to an average of 4.0-4.2 fish per mile of river in the upper reach. In the lower reach, population estimation included subadults as well as adults. Size of the population there, averaged over a three-year period, was estimated to be 344 individuals (95% C. I. = 196-604) using program CAPTURE; using program RECAP, the estimate was 385 (C. I. = 202-733). These point estimates equate to an average of 3.1-3.4 fish per mile in the lower reach. For the river as a whole, size of the subadult and adult population was probably around 600-650 during the period of study.

A large number of young Colorado squawfish (primarily 300-400 mm long) were found in the lower reach, downstream of Moab, during 1991. Scale analysis indicated these fish were from three year-classes hatched in 1985, 1986, and 1987. By 1992, these fish were distributed throughout the river system. Trammel-netting catch-per-unit effort in the upper reach steadily increased over the four years of study. Though catch rates of larger adults (> 550 mm long) did not significantly increase, catch rates of subadults and young adults (< 550 mm long) increased five-fold. Size-frequency analysis of lower-reach fish indicated the 1985-1987 cohorts were the strongest year classes produced since at least 1977, and no similarly strong year classes have been produced since 1987. Catch rates of larvae and YOY in the Grand Valley also indicated that reproductive success in 1986 and perhaps in 1987 was relatively high, and all other years through 1994 had comparatively low catch rates.

Until this recent pulse of young adults was produced, the vast majority of adults were found in the upper reach; the lower reach contained almost exclusively individuals < 500 mm long. Thus, in recent years, the bulk of the adult population was contained in the upper reach. Within the upper reach, very few individuals < 450 mm long are found, indicating that recruitment to the upper reach subpopulation occurs almost entirely from colonization of young adults migrating there from the lower reach. In contrast, size frequencies recorded during the mid 1970's indicate that significant recruitment in the upper reach may formerly have occurred via young rearing within the upper reach.

Though some level of recruitment appears to occur every year, the Colorado River population of Colorado squawfish is probably sustained by strong year classes that occur very infrequently. Though survival rate is likely fairly constant from one year to the next,

recruitment is highly variable. Long-term, average, annual rates of recruitment are unknown and therefore it is difficult to discern whether recruitment balances mortality over the long term. Given the current low population size in comparison with historical accounts that suggest the species was formerly abundant, it is likely that recruitment has not kept pace with mortality. However, this population appears quite capable of recovering on its own if the frequency of strong year classes can be increased. This will require the improvement of environmental conditions that currently limit reproductive success and survival of young. Any increase in adult survival rates would also be beneficial.

INTRODUCTION

Populations of Colorado squawfish (*Ptychocheilus lucius*) historically occurred throughout warm-water reaches of the Colorado River basin from Wyoming, Utah and Colorado south to the Gulf of California (Miller 1961). By the 1970's they were extirpated from the entire lower basin (downstream of Glen Canyon Dam) and portions of the upper basin as a result of major alterations to the riverine environment (Moyle 1976). Today this species persists only in the upper basin. Having lost some 80% of its former range it was federally listed as an endangered species in 1967 (Federal Register 32 [43]: 400).

In the upper basin, the Colorado, Green, and San Juan rivers and associated tributaries comprise the remaining range. Currently, the Green River and its two large tributaries the White and Yampa rivers support the most viable population (Tyus 1991), while the San Juan River contains the most diminutive population (Platania et al. 1991). In the upper Colorado River, a population persists but catch rates of adults and young are relatively low (Valdez et al 1982, Osmundson and Kaeding 1989, McAda et al. 1994).

Our objective was to assess the current status of the Colorado River population and to relate that status to past and future trends, both short and long term. To do so, we attempted to 1) estimate the size of the adult population, 2) determine the extent or frequency of reproduction and recruitment, 3) identify any recent trends via changes in age or size structure over time, and 4) examine historical accounts for clues to former abundance. To accomplish items 1, 2 and 3 above, we conducted a systematic, river-wide study aimed at capturing and marking adult and subadult Colorado squawfish over a four-year period. For item 2, we also monitored reproductive success in one portion of the river by sampling larvae and young-of-the-year (YOY) abundance over a nine-year period. For item 3, we also examined size-frequency data collected by other researchers as far back as 20 years ago. Other available data sets were utilized in various ways and our findings were integrated with those of other researchers.

Assessment of future trends, though speculative by nature, are requisite to recovery planning; we therefore provide a discussion on the likelihood of population persistence based on what is currently known regarding limiting factors and current trends in habitat alteration and planned recovery activities.

STUDY AREA

Background

Upon hatching, Colorado squawfish larvae drift downstream and are soon widely distributed. During summer they can be collected with seines from backwaters and other low-velocity habitats where they largely remain through the postlarval phase (Haynes et al. 1984, Tyus and

Haines 1991, McAda and Kaeding 1991). By fall, many YOY in the Colorado River become concentrated in the lowermost 103 km where gradient is low and sand-bar-formed backwaters are most plentiful; here they rear through the juvenile phase (McAda et al. 1994). After attaining ≈100 mm in length, Colorado squawfish are infrequently collected; however, once > 250 mm long, they become susceptible to trammel netting and electrofishing. Capture rates of these juveniles or their percent frequency in the population are good indicators of year-class strength. Evidence of recent strong year classes are therefore best detected in these lower reaches. As these young fish mature they become widely distributed, ostensibly seeking better habitat as their food requirements change, with many eventually returning as adults to upstream reaches.

Extent of Study Area

Our study area for subadult and adult Colorado squawfish included the entire occupied portion of the Colorado River mainstem upstream of the Green River confluence, as well as the lowermost portion of the Gunnison River (Fig. 1). Colorado River locations are described in river kilometers (RK) upstream of the Green River confluence, Utah (RK 0.0); kilometers were converted from river miles mapped by Belknap and Belknap (1974). The Colorado River study area extended upstream to RK 298.1 at Palisade, Colorado, where further upstream movement of fish is blocked by two diversion dams. The Gunnison River portion extended only 3.5 km upstream from the confluence with the Colorado River (RK 275.1) to the base of the Redlands Diversion Dam where further upstream movement of fish was also blocked.

Based on the distributional pattern of adults and juveniles, we partitioned the study area into two major reaches, upper and lower, and three subreaches within the upper reach. The lower reach extended from the bottom of the study area upstream to the lower end of Westwater Canyon (RK 181.0); the upper reach, from the top of Westwater Canyon (RK 200.0) to the top of the study area. Westwater Canyon was excluded because of the difficulty in sampling there and because recent studies indicate few Colorado squawfish are found there (McAda and Kaeding 1991, Tom Chart, UDWR, personal communication). To examine distribution of adults within the upper reach, three sub-reaches were identified based on discharge, average gradient, and landform type. The upper subreach (RK 298.1-275.1), located in an alluvial valley, has a mean discharge of 110 m^3/s, and an average gradient of 1.70 m/km; the middle subreach (RK 275.1-245.5), also located in the alluvial valley, has a mean discharge of 175 m^3/s and an average gradient of 1.27 m/km. The lower subreach (RK 245.5-200.0), like the middle subreach, has a mean discharge of 175 m^3/s, but is largely canyon bound and has a lower average gradient (0.91 m/km).

To sample larvae and YOY, our study area was confined to the Grand Valley in Colorado (RK 298.1-245.5). In addition, larvae were also sampled in the aforementioned 3.5 km reach

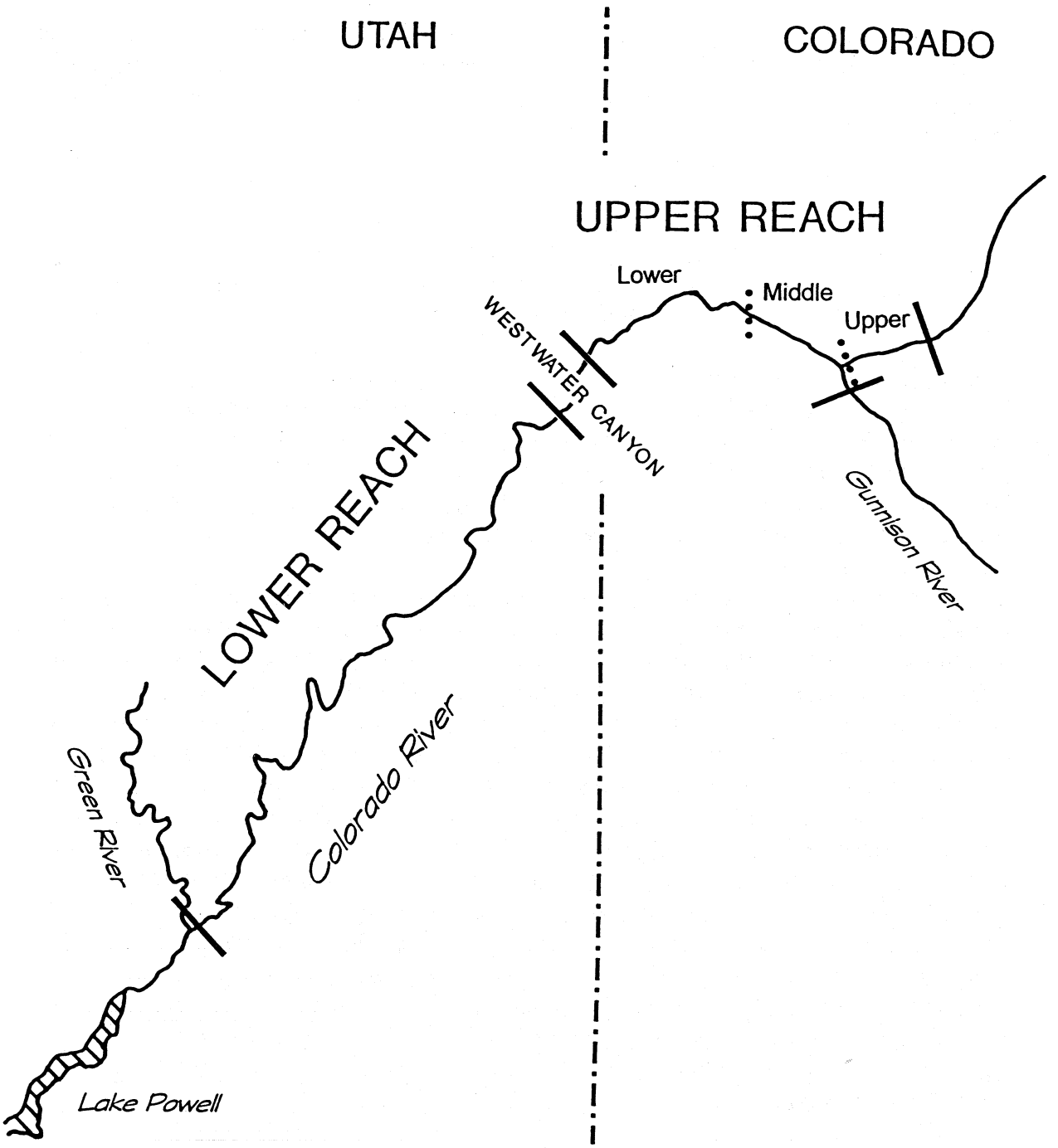


Figure 1. Map of the upper Colorado River study area. The area is divided into two major reaches: an upper and lower. The upper reach is divided into three subreaches: lower, middle and upper. The two bars demarcating upstream boundaries on the Colorado and Gunnison rivers represent physical barriers to upstream fish movement. No similar barrier exists at the lower end of the study area at the Green River confluence.

of the Gunnison River; however, backwaters were not available in this reach for YOY seining. Although we did not sample the lower river reach, seining surveys for YOY are conducted there as part of the Interagency Standardized Monitoring Program (ISMP) on an annual basis (see McAda et al. 1994).

METHODS

Subadults and Adults

Capture Efforts

During 1991 through 1994, an intensive effort was made each spring to capture subadult and adult Colorado squawfish by systematically sampling the entire study area. During late April to mid June, trammel nets were used to capture subadults and adults from backwaters. Colorado squawfish are attracted to these calm habitats during spring runoff when discharge in the main channel dramatically increases (Osmundson and Kaeding 1989).

Upon approaching a backwater in a 4.3-m-long, jon boat, a net-person stationed at the bow would attach one end of a net to the shore on one side of the backwater mouth; the boat operator would then quickly back the boat across the mouth and swing the bow forward so the net person could jump off on the opposite bank keeping tension on the remainder of the net. This effectively trapped fish inside the backwater. The boat and driver then entered the backwater by passing over the net with the motor raised. Once inside, the boat was used to scare fish toward the channel; it was vigorously motored back and forth starting at the far end of the backwater and working towards the mouth. As fish fled, they became ensnared in the net; hence, the technique was dubbed 'scare and snare' and proved to be extremely effective. In very large backwaters or flooded ponds, additional nets were set once the mouth was blocked. The net or nets were pulled as soon as sufficient 'scare' effort was expended (5-15 min). Ensnared Colorado squawfish were placed in a live well until all fish were removed from the nets. When numerous nets were set in one backwater, 1-2 hr would sometimes elapse before the last net was pulled. Trammel nets of various lengths were 1.8 m deep with a 2.5-cm bar mesh and a 25-cm-mesh outer wall. After the first year, a finer mesh net (1.3-cm bar mesh x 18-cm-mesh outer wall) was used in the lower reach to prevent small Colorado squawfish from becoming gilled.

Three passes through the upper-reach study area were made each spring. With each pass, we netted every backwater we suspected adult Colorado squawfish might use. Each pass would generally take 7-9 d to complete. In the lower reach, two passes were made each spring (except in 1991 when only one pass was made). In some portions of both reaches where backwater habitats were rare, both shorelines were electrofished with a 4.9-m-long, jon boat equipped with a variable voltage pulsator (Coffelt VVP-15) using pulsed DC current. In the upper reach, some of the passes through the lower subreach were supplemented with capture

data provided by the Colorado Division of Wildlife (CDOW), collected as part of the ISMP. Passes through the lowermost 3.5 km of the Gunnison River were supplemented with capture data from a concurrent U. S. Fish and Wildlife Service (USFWS) electrofishing survey of that river (Burdick 1996); the short reach there is open to and used by Colorado squawfish from the Colorado River but contained only one backwater during spring.

Colorado squawfish were scanned for the presence of a passive integrated transponder (PIT) tag, and marked with one if none was found. PIT tags were implanted in the body cavity using a hypodermic needle after fish were anesthetized with Tricane methanesulfonate. Each PIT tag had a unique, 10-digit, alpha-numeric code that was read with an electronic scanner and recorded in the field. The insertion site for the tag was 2-5 mm posterior to the base of the left pelvic fin. Maximum total length (TL), as defined by Anderson and Gutreuter (1983), was measured and fish were released after recovery from the anesthetic.

Survival Rate, Abundance, and Recruitment Estimation

Upper Reach. Our capture-recapture data from the multiple passes through the study area were used for estimating, and making inferences about, survival rates (in particular), and abundance and recruitment (to a limited extent) based on open, capture-recapture models. 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 within years to estimate population abundance. For an overview of models and analysis methods based on open- and closed-model, capture-recapture data see Nichols (1992) and Pollock et al. (1990).

We assumed the Cormack-Jolly-Seber (CJS) model (see Lebreton et al. 1992) as our starting point to estimate survival rates. In so doing, no assumptions were needed about abundance or recruitment, or trends in population abundance. The CJS model is based on two types of parameters: survival rates, denoted ϕ and capture probabilities, p. These parameters may vary by occasion and by time intervals between capture occasions. Thus, with 12 capture occasions (upper reach), the estimable parameters in the basic CJS model are survival rates ϕ_1 to ϕ_{10}, occasion-specific capture rates p_2 to p_{11} and the product $\phi_{11}p_{12}$ (21 parameters). There is a large literature on CJS models, data analysis based on such models, and analysis strategy, including model selection (e.g., Buckland 1980, Burnham et al. 1987, Pollock 1982, Pollock et al. 1990, Lebreton et al. 1992, Burnham and Anderson 1992, Anderson et al. 1994, Burnham et al. 1995). We based our analyses on this literature; hence, we give here only minimal information on methods.

The analysis strategy is to first determine if the general Cormack-Jolly Seber model fits the data. Program RELEASE (Burnham et al. 1987) is used to compute the goodness of fit of the time-specific CJS model for our capture data. If fit is acceptable, then program SURGE (Lebreton et al. 1992) is used to find the best model out of a set of several models considered. Such models correspond to restrictions on the parameters in the starting CJS model. For

example, perhaps having all $p_i \equiv p$ (capture probability is the same on every occasion) is an adequate model; or perhaps capture efficiency improves with time so a model considered would be logit $(p_i) = \log(p_i/(1-p_i)) = a + b \cdot i$. The philosophy and reasoning supporting this approach is linked to ideas of what is an adequate and justifiable model and how we select such a model.

We used Akaike's Information Criterion (AIC) for model selection (Akaike 1973, Lebreton et al. 1992, Burnham and Anderson 1992, Anderson et al. 1994, Burnham et al. 1995) given the set of models considered. The models considered (in general terms) were the fully time-specific CJS model (21 parameters) and simpler models based on a mixture of features: constant per-unit time survival rates, year-specific survival rates, season-specific survival rates, capture rates that could be year- or season-specific, or constant, or show a linear trend on either occasion or year. AIC is a relative measure (computed for each fitted model) of how appropriate (i.e., "best") a model is for a given set of data. The best model has the smallest AIC (AIC_{min}); "best" is a trade off between precision and bias (Burnham and Anderson 1992). For a given set of data and models it is the differences in the AIC values, compared to the AIC-best model, that are most informative. These differences are denoted as ΔAIC; thus, $\Delta AIC = AIC_i - AIC_{min}$. Any model within about $\Delta AIC = 2$ can be considered as a plausible model for the data. The larger the ΔAIC, the less plausible the model ($\Delta AIC > 4$ seems a useful guide for implausible models in this application).

When time intervals are not equal (as here), the constant per-unit-time survival rate model uses

$$\phi_i = \phi^{\Delta_i},$$

where Δ_i is the time interval (as a fraction of a year) between capture occasions i and $i + 1$ and the basic survival parameter in the model is ϕ, herein expressed as an annual survival rate. A capture pass ("occasion") of the study area (e.g., upper Colorado River area) required 6 to 10 days to complete (and these days could be spread over a three week period). To define the instantaneous time point (t_i) for occasion i we used a weighted average Julian-date day. Each pass recorded the number of fish, n_j, caught on day j within that pass. Hence, we used average capture time within a pass as t_i:

$$t_i = \frac{\sum j \cdot n_j}{\sum n_j}$$

Given these t_i as the capture occasion "times," then $\Delta_i = t_{i+1} - t_i$.

It is important to understand that the survival rates, ϕ, in capture-recapture models are apparent survival probabilities. In general, $\phi = S(F)(1-L)$, where F (fidelity) is the probability that a fish returns to (or stays in, if non migratory) the river stretch being sampled, and L is the tag loss probability. Given that this study used PIT tags, we expect little or no tag loss or tag failure; it is reasonable to take here $L = 0$. If fidelity is 1, then estimated survival rate (ϕ) is an estimator of physical survival rate (S). The converse of S, 1- S is actual total mortality

during the reference time period. All survival rates here have been put on the basis of one calender year.

The analysis with the CJS models has two objectives: (1) find a best model for, hence best estimate of, survival rate (ϕ may vary by time); (2) find a best model for capture probabilities, p. With regard to p we are especially interested in presence or absence of trends in capture probabilities in order to separate any such trends from trends in population abundance. AIC-based model selection was used to accomplish both objectives.

The models considered are based on the main possible sources of variation in ϕ and p. Following notation of Lebreton et al. (1992) we denote full time variation in parameter-types in the models by ϕ_t and p_t. Thus, model $\{\phi_t, p_t\}$ has 21 estimable parameters here. If there is no time variation in a type of parameter it is denoted as ϕ or p. Hence, model $\{\phi, p\}$ has two parameters. Intermediate models include $\{\phi_t, p\}$ and $\{\phi, p_t\}$ (both with 12 parameters). To denote capture rate being the same within year (i.e., for the three within-year capture occasions) we use the notation p_{year}. For example, the model $\{\phi, p_{year}\}$ has 5 parameters: one annual survival rate ϕ, and four capture probabilities, one in each year.

Survival rates (on a per-unit-time basis) might be different in spring from the rest of the year. Hence, we considered a model with ϕ varying by "season," where season here denotes three time intervals for the upper Colorado River segment (two intervals for the lower segment): from occasion 1 to 2 within a year and occasions 2 to 3 within a year (periods of about 0.06 of a year) and then the other (about) 0.88 of a year to the next annual sampling period (late April to mid June). The notation $\phi_{seasons}, p)$ denotes a model with 4 parameters.

We considered that survival rates might be the same in both short intervals but different from the longer time interval, denoted $\phi_{short/long}$. For example, the model $\{\phi_{short/long}, p\}$ has 3 parameters: a constant capture rate and survival rate during spring (roughly) different from the rest of the year. We also explored whether a useful model might assume survival rate was 1 during the short time intervals. This motivates fitting a model that forces the short period survival rates to be 1, denoted $\phi_{short=1/long}$, hence a model such as $\{\phi_{short=1/long}, p_{year}\}$, which has 5 parameters.

It was necessary to determine if there was evidence of a trend in capture rates in order to assess time trends in abundance from numbers caught. This motivates fitting models with a linear trend on capture occasion in p, denoted p_T. The capital "T" is distinct from a lower case "t" that denotes arbitrary time variation in capture rates (this notation has been used before, see Burnham et al. 1996, Franklin et al. 1996); hence we can have models such as $\{\phi, p_T\}$ which allows capture rate to vary linearly on capture occasion (not on time as such, but on occasion); it has 3 parameters.

Finally, capture rates might be the same within year, but change over years in a linear way. We use p_Y to denote this sort of modeled effect (based on a logit link). This model is using

capture probability at any occasion within year Y as logit $(p) = a + b \cdot Y$ ($Y = 1, 2, 3, 4$). Thus there are models such as $\{\phi, p_Y\}$, which has 3 parameters.

Another parameter of interest is abundance, $\hat{N}$, of the sampled population at each capture occasion. Population size may vary by year and we want to know if $\hat{N}$ is stable, increasing, or decreasing. Jolly-Seber models can be used to estimate population size. However, our data are too sparse to get useful occasion-specific estimates of N based on open-model methods (such as with program JOLLY, Pollock et al. 1990). Instead, we used closed-model methods (i.e., program CAPTURE, Otis et al. 1978, White et al. 1982) based only on captures and recaptures for the three occasions within a year to estimate abundance by year. This analysis assumes population closure over a time period of about 6 weeks. However, this assumption was not shown to be violated based on the capture data; hence, closed methods are judged by us to be acceptable for getting yearly spring estimates of $\hat{N}$. The simplest model (the null model) of program CAPTURE was used to get $\hat{N}$ (by year). This model assumes the same capture rate, p, applies at each occasion within year, but p may vary by year. The choice of this model was partly based on analyses with SURGE that supported constant within-year p, was partly motivated by the sparseness of the data, and was supported by the model selection algorithm in CAPTURE that suggested for each year the use of this simplest model.

A modified open population analysis method (program RECAP, Buckland et al. 1980) was used as a consistency check for average population abundance over the four years, average annual survival rate, and to obtain some information about average annual recruitment rates into the sampled population. Equally important is that program RECAP computes standard errors and confidence intervals on these estimated averages by use of a nonparametric bootstrap method, hence the intervals are robust to parametric model assumptions.

Estimates of numbers of fish recruited by year (B) were made. The three types of annual population parameters are related by

$$\hat{N}_{i+1} = \hat{N}_i \phi_i + B_i,$$

where B_i is recruitment of new (unmarked) fish into the sampled population at year i. Program RECAP is especially useful at providing robust estimates of B because that program implements constrained model Jolly-Seber estimators, which can be important for sparse capture-recapture data such as these.

Standard linear regression (SAS Institute 1985) applied to numbers of fish captured by occasion, n_i, was used to test for trend over years in fish abundance without information on a possible trend in capture rates. Although the latter is supplied by the CJS-based analyses of the full capture data, the results of such regressions help determine whether trends in Colorado squawfish abundance existed during the four years of study.

Lower Reach. Methods used to estimate survival rate and abundance of subadults and adults in the lower reach were generally the same as that outlined above for the upper reach. The only difference was that there were two passes, or sampling occasions, per year instead of three and only one in 1991. Hence, abundance estimates could only be made for 1992, 1993 and 1994.

Size Frequency Analyses

To detect change in age structure we compared size frequency histograms produced from our length data with those produced from earlier, published (Seethaler 1978) and unpublished (USFWS, Grand Junction field office data files), capture records. Length data were grouped by year and placed within 50-mm length categories. Because the number of captures among years were not distributed consistently over the length of the upper reach, where most adult-sized fish were captured, we first tested for differences in size distribution among samples from the three major subreaches (combined 1991 through 1994 data) using Kolmogorov-Smirnov 2-sample tests. Because significant differences in size distribution were found between the upper subreach and the lower two, we partitioned data by subreach when making year-to-year comparisons. Length data from the lower 2.2 miles of the Gunnison River were not included in any subreach. Though there was no significant difference between the middle and lower subreach, we kept analyses separate because most captures in the lower subreach were by electrofishing, which tends to skew size distributions to the right (Osmundson et al. 1996). A minimum of about 30 different fish were found to be needed to develop meaningful length frequencies such that additional data do not result in significant histogram changes (Fig. 2). Because a stable age distribution during the 1982-1995 period of record was already reported for adults > 550 mm (Osmundson et al. 1996), our analysis focused on changes in capture frequencies of younger adults and juveniles to assess recruitment.

Data sets were available from 1979 to 1995; however, apart from the recent data, only samples from 1979 and 1982 had more than 30 fish from the upper reach. Sample size was inadequate in all earlier years for the lower river reach. For comparisons among time periods for a given upper river subreach, data from two consecutive years often had to be pooled to obtain adequate samples (Tables 1 and 2). Older data (1974 through 1976) were also obtained by taking length points from a length-weight plot provided in Seethaler (1978). Unfortunately, data from the three years were combined for the plot and raw data for the individual years could not be obtained (Karl Seethaler personal communication). Because of the importance of this early data, we used the 3-year pooled data in our comparisons.

Kolmogorov-Smirnoff 2-sample tests were used to identify changes in size distributions among sampling periods. Test of proportions was used to identify changes in proportions of particular size groups between sampling periods. Most captures during 1979 occurred in the lower subreach using electrofishing. To compare size frequencies for that year with recent years, we pooled our recent lower-subreach data for years 1991 and 1992 and for years 1993 and 1994. During 1982, most captures were evenly divided between the upper and middle subreaches and separately were fewer than our goal of a 30-fish minimum. The 1991 and

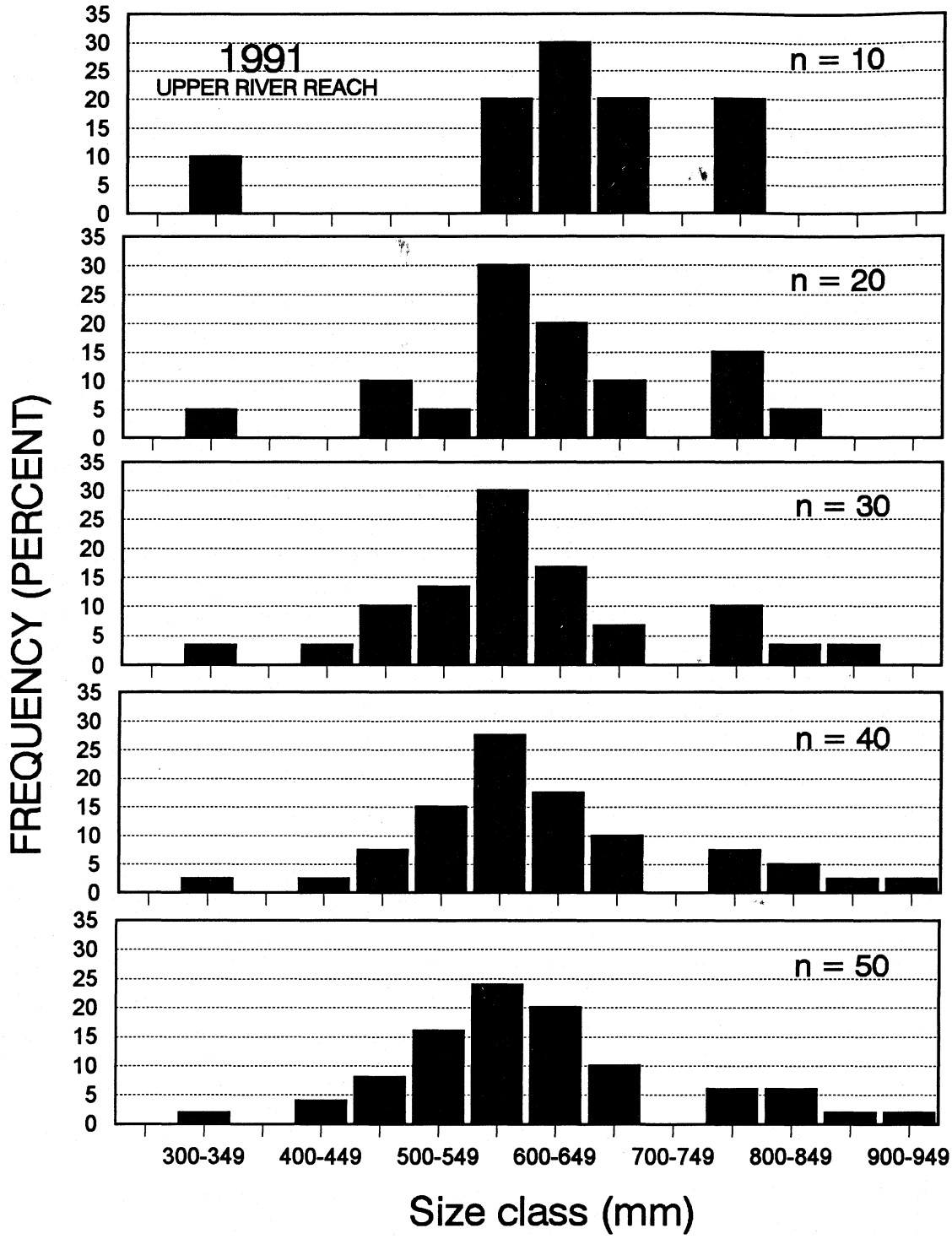


Figure 2. Effect of sample size on length-frequency histograms. Graphs are of Colorado squawfish lengths from the upper reach during one time period (1991). Lengths for top graph are from first 10 individuals captured; lower graphs depict change by adding lengths of successive captures in increments of ten.

Table 1. Number of Colorado squawfish lengths available for size frequency comparisons partitioned by year and subreach within the upper reach. Recaptures of the same fish within a subreach during a given year are not included.

	Year							
Subreach	1974-1976	1979	1982	1991	1992	1993	1994	1995
Lower	0	33	9	22	7	16	12	0
Middle	66	7	23	13	32	41	37	53
Upper	0	4	23	23	21	17	21	0

Table 2. Year and reach combinations used for comparisons of length frequencies through time. For each reach, length frequencies were compared among years or groups of years. Years grouped together indicate data for those years were pooled.

Upper subreaches				
Upper	Middle	Upper-Middle	Lower	Lower Reach
1991	1974	1982	1979	1991
1992	1975			
	1976	1991	1991	1992
1993		1992	1992	
1994	1991			1993
	1992		1993	
			1994	1994
	1993			
	1994			
	1995			

1992 data sets, when pooled, were also evenly divided between the upper and middle subreaches. Thus, to make the most valid early-to-recent comparison, the upper and middle subreach data were combined and the 1982 set compared with the pooled 1991 and 1992 set.

Data from 1974-1976 were from the middle subreach and were therefore compared with recent data from there only. To look for evidence of recent recruitment in these upper reaches, we compared pooled 1991 and 1992 data with pooled 1993 and 1994 data for each of the three subreaches separately. For 1995, data were also available from another study (Mourning 1995), but only for the middle subreach. We also examined recent length frequencies of lower-reach fish, i.e., from RK 0.0 to 181.0. Table 2 shows year and reach combinations used for comparisons.

Catch per Unit Effort

Catch per unit effort (CPUE) of adults in the upper reach was compared among years (1991 through 1994) as an additional means to determine if the population increased in size during the years of study. CPUE was calculated using the mean number of fish caught per net set as the unit of measure. Size of sampled backwaters varied greatly with location and flow level and thus effort among net sets was not constant; however, average effort per net set was assumed constant among years. A Kruskal Wallace non-parametric Analysis of Variance (ANOVA) was used to test for CPUE differences among years.

Reproductive Success

We collected samples of fish larvae and samples of YOY (1986 through 1994) to monitor annual reproductive success of Colorado squawfish and distribution of young in the Grand Valley (middle and upper subreaches). The study area was subdivided into 18 3.2-km sections and one sample of larvae was collected weekly from each section during early-to-mid-July through the end of August. Each sample was collected from either a backwater, embayment or shoreline habitat using a 0.6-m-wide, 0.5-mm-mesh, hand seine. Sampling sites selected within each section changed weekly. Sampling effort was not constant among sites (5-15 minutes of seining per site), but average effort per site was assumed constant among years. Mean number of Colorado squawfish larvae per sample was the unit of measure.

YOY were sampled once yearly in late September or early October by seining backwaters with a 4.6-m-wide, 3-mm-mesh, beach seine. The study area was subdivided into 8-km sections and two samples were collected from each of two backwaters within each section. The surface area covered by each seine haul was recorded. YOY (and larval samples) were preserved in 10% formalin and sent to the Larval Fish Laboratory at Colorado State University for identification. Mean number of YOY per 100 m^2 seined was the unit of measure. Because of the non-normal distribution of fish captures, CPUE was calculated as a geometric mean: fish/100 m^2 was first log-transformed for each sample using ln (fish/100m^2 + 1), the anti-log of the mean taken, and one subtracted from the result. Kruskal-Wallis one-

way ANOVA was used to test for differences in CPUE among years and the Kruskal-Wallis multiple comparison z-value test was used to identify years with significantly different CPUE.

Others Studies

To fill in information gaps for years or portions of river for which we had no data, we reviewed agency reports and integrated pertinent findings with ours. These included a USFWS, river-wide, annual sampling program for Colorado squawfish larvae and YOY during 1982-1988 (McAda and Kaeding 1989) and the ISMP, which annually samples YOY and adult Colorado squawfish in selected reaches of the Colorado River. Results from the ISMP during 1986-1992 are summarized in McAda et al. (1994).

RESULTS

Adult Survival Rate, Abundance, and Recruitment Estimates

Upper Reach

The two best models (lowest AIC values), differing by only 0.034 AIC units, provided annual survival rate estimates of 0.845 and 0.860. The best model as determined by AIC (Table 3) has constant capture rate on each occasion (p = 0.107, SE = 0.014), survival rate set to 1 in the short periods among sampling occasions in the spring, and constant survival (ϕ = 0.845, SE = 0.076) the remaining portion of the year. The next best model (constant ϕ all year, constant p) is more credible biologically as it is unlikely there is no mortality during late April to mid June. For this model, the annual survival rate is ϕ = 0.860 (SE = 0.069). A 95% confidence interval on ϕ was computed here based on a logistic transform of ϕ and is 0.662 to 0.950 (the usual interval based on $\phi \pm$ 1.96 SE is not credible). Table 3 shows notation for the survival models fitted to the upper reach capture-recapture data.

Because we were interested in whether the sampled population was stable, increasing or decreasing during the four years of study, it was important to consider models with time trends in capture rates. Models with ϕ constant and linear on logit-p on occasion or linear on year are the next best models. For model $\{\phi, p_Y\}$, ϕ = 0.841 (SE = 0.072) and p_Y (SE) = 0.093 (.020), 0.102 (0.015), 0.112 (0.015), and 0.123 (0.023) for 1991, 1992, 1993, and 1994, respectively. This shows an estimated annual rate of increase in capture probabilities of 10%. The increase in capture rates is not statistically significant (z-test = 0.914, P = 0.3607, two-sided test), as corroborated by the small ΔAIC (= 1.2) value. Still, in judging possible increases in the sampled population it would be conservative to consider that capture rates increased 10% per year.

Table 3. Capture-recapture open models fit to the upper Colorado River capture data. Also shown are the number of estimable parameters in each model (K), AIC values and AIC increments (ΔAIC) compared to the AIC best model, sorted by AIC value, smallest (best model) to largest AIC (worst model).

Model	K	AIC	ΔAIC
$\{\phi_{short\ =\ 1/long}, p\}$	2	723.776	0.000
$\{\phi, p\}$	2	723.810	0.034
$\{\phi, p_Y\}$	3	724.976	1.200
$\{\phi, p_T\}$	3	725.207	1.431
$\{\phi_{short/long}, p\}$	3	725.772	1.996
$\{\phi_{season}, p\}$	4	726.061	2.285
$\{\phi_{short\ =\ 1/long}, p_{year}\}$	5	726.400	2.624
$\{\phi, p_{year}\}$	5	726.439	2.663
$\{\phi, p_t\}$	12	734.370	10.594
$\{\phi_t, p\}$	12	736.651	12.875
$\{\phi_t, p_{year}\}$	15	738.859	15.088
$\{\phi_t, P_t\}$	21	747.348	23.572

Model $\{\phi_{short/long}, p\}$ estimated the survival rate in the short intervals between sampling occasions as about 0.99. Thus, closed models seem useful to apply to the data separately by year to estimate population size.

Table 4 gives the results from model M_0 (constant within-year capture probabilities) computed by CAPTURE. The separate annual population size estimates (they are independent over years) are too imprecise to be useful to assess trends. It is better to just average these estimates and conclude that our best estimate of average annual population size in these four years is $\hat{N} = 253$ (SE = 41) with a 95% confidence interval of 161-440.

Program RECAP (Buckland 1980) was used as a consistency check on these results and to get some inference about possible recruitment in the sampled population. That program is not as sophisticated as RELEASE, SURGE and CAPTURE, but does compute robust variance estimates. Results from RECAP: average annual abundance, $\hat{N} = 263$ (SE = 38), 95% C.I. 186 to 333; average annual survival rate, $\phi = 0.822$, 95% C.I. 0.611 to 0.922; average annual recruitment, $B = 40$ (SE = 10), 95% C.I. 24 to 59. These results are consistent with results from SURGE and CAPTURE, and support the idea of a stable population (mortality balances recruitment in RECAP results, this balance is not a forced result), during the four years of study, while not denying the possibility of the population increasing during this time.

Table 4. Yearly population size estimates for the upper reach, based on Model M_0 (constant within-year capture rates) from program CAPTURE. Also shown are theoretical standard errors and 95% confidence intervals (profile likelihood) by year, and estimated mean abundance, its empirical standard error and a 95% confidence interval, based on a shifted log-transform, and a t_3-distribution. Capture rate estimates from CAPTURE are also shown.

Year *I*	$\hat{N}_i$	SE	95% CI	*P*
1991	205	68.1	124 to 520	0.106
1992	311	125.3	179 to 1204	0.074
1993	163	29.5	121 to 246	0.194
1994	332	90.1	223 to 728	0.103
Mean	253		161 to 440	
SE	40.8			

Table 5 presents several data summaries that bear on the matter of whether there might have been a trend in the upper reach subpopulation during the years of study. First we looked at the number of fish (n) captured by occasion and year. A standard linear regression against year was done on these twelve numbers to estimate a linear yearly trend. If we assume capture probabilities are constant over occasions and years, then this is a test for trend in population abundance. The slope estimate was a 17.1% increase per year ($P = 0.001$, two sided t-test, 10 df), 95% C.I. 8.5% to 24.6%. However, our best estimate (and it has uncertainty) of a possible trend in capture rates is about 10%; thus, to be conservative we would estimate a population increase of about 7% per year during 1991 through 1994. This number has substantial uncertainty that we are not now able to quantify.

Annual abundance, $\hat{N}_Y$, can be computed even if the upper reach subpopulation was increasing and capture probabilities were increasing during the period of study. In Table 5, M_Y is the number of distinct fish captured (whether once or more) by year. From open model $\{\phi, p_Y\}$, Table 5 shows the estimated capture rate per occasion, by year, p_Y. The probability of catching a fish (once or more) that is present in a year is just $p(M_Y) = 1 - (1 - p_Y)^3$, which is shown in Table 5. The best estimator of abundance by year allowing this trend in capture rates is $\hat{N}_Y = M_Y / p(M_Y)$; these values are shown in Table 5; they do average to 254 but reflect an increasing abundance over the four years.

Lower Reach

Estimates in the lower reach include not only adults, as in the upper reach, but also subadults as small as 265 mm TL. However, the vast majority of captures were of individuals > 300 mm TL (see section below on size frequency). Program RECAP provided an estimate of

Table 5. Number of Colorado squawfish captured by occasion (including recaptures) and year (n), and the number of different individuals captured by year (M_Y). Other quantities are explained in the text.

n	Year			
Occasion	1991	1992	1993	1994
1	23	21	31	27
2	17	25	31	37
3	25	23	33	38
n	21.7	23.0	31.7	34.0
Quantities				
M_Y	59	65	78	93
p_Y	0.093	0.102	0.112	0.123
$p(M_Y)$	0.254	0.276	0.300	0.325
$\hat{N}_Y$	232	236	260	286 (ave N_Y = 254)

average abundance over the three-year period (1992-1994) in the lower reach of $\hat{N} = 425$ (SE = 144), 95% C. I. 196-732. However, RECAP assumes that time intervals between occasions are all equal (within-year intervals were similar to each other but not to among-year intervals); this results in some not-optimal weighting when the program takes an average across years. A better weighting produced an estimate of $\hat{N} = 385$ (SE = 130), 95% C. I. 202-733.

With program CAPTURE, model M_t was used to estimate abundance within years. Results for the three years with two within-year sampling passes were: $\hat{N} = 224$ (SE = 155) for 1992, $\hat{N} = 512$ (SE = 228) for 1993 and $\hat{N} = 297$ (SE = 126) for 1994. An average estimate for the three-year period was $\hat{N} = 344$ (SE = 101), 95% C. I. 196-604.

From RECAP, there was indication of recruitment over the three-year period (average B = 118, SE = 74), but abundance estimates suggest that recruitment likely only occurred between 1992 and 1993 with an increase of several hundred fish. From SURGE, the point estimate of average annual survival rate was $\phi = 0.57$, 95% C. I. 0.34-0.95. The RECAP-derived estimate was $\phi = 0.43$, 95% C. I. 0.15-0.78. Because of the wide standard errors, neither estimate is particularly useful. However, both estimates indicated a considerably lower apparent survival rate than that in the upper reach. This would be consistent with fish emigrating to adjacent reaches if their actual physical survival is similar to that of fish in the upper reach. Whether these younger fish might experience natural mortality rates somewhat lower than upper-reach adults is unknown.

Adult Size Frequency Analysis

Lower River Reach

We found a relatively large number of young fish in the lower reach during 1991 and subsequently tracked the growth and distribution of this group through 1994 (Fig. 3). Scale analysis indicated this pulse of fish was composed of three consecutive year classes, with much overlap in size (Table 6). Subsamples from fish of this group captured in 1991 (N = 14) and 1992 (N = 21) were aged using scale analysis (see Osmundson et al. 1996 for methods). The aged fish from 1991 were 325-379 mm long; those from 1992, 326-479 mm long. In addition, scales were collected from two smaller fish, 259 and 307 mm long. From a total sample of 37 fish, 22% had hatched in 1985; 46%, in 1986; 27%, in 1987; 5%, in 1988. Though these percentages may or may not reflect the actual proportions of each age class in this group, it is clear that a strong year class was produced in 1986, and we suspect that 1985 and 1987 were also relatively strong year classes.

There were few fish present in the lower reach during our study that were larger (older) or smaller (younger) than the 1985-1987 year classes (Fig. 3). This group dominated the lower river subpopulation beginning at least as far back as the first year of study, 1991, and through the last year, 1994. Based on our results, a strong year class should be evident from length-frequency histograms during a five year period between four and nine years after it is produced (1987 year-class was first detected in 1991; 1985 year-class was still evident in 1994). From this we can assume that no similar strong year classes were produced for at least three years prior to 1985 and none produced for at least three years following 1987. In addition, McAda et al. (1994) reported that spring electrofishing catch rates had been relatively low in this portion of the river at least 5 years prior to the initiation of our study.

Table 6. Ages of young Colorado squawfish of various sizes as determined by scale analysis.

Year collected	Size range	N	Age (years)	Year class
91	259	1	3	88
91	325-374	3	4	87
91	332-383	9	5	86
91	375-379	2	6	85
92	307	1	4	88
92	326-452	7	5	87
92	412-472	8	6	86
92	430-479	6	7	85

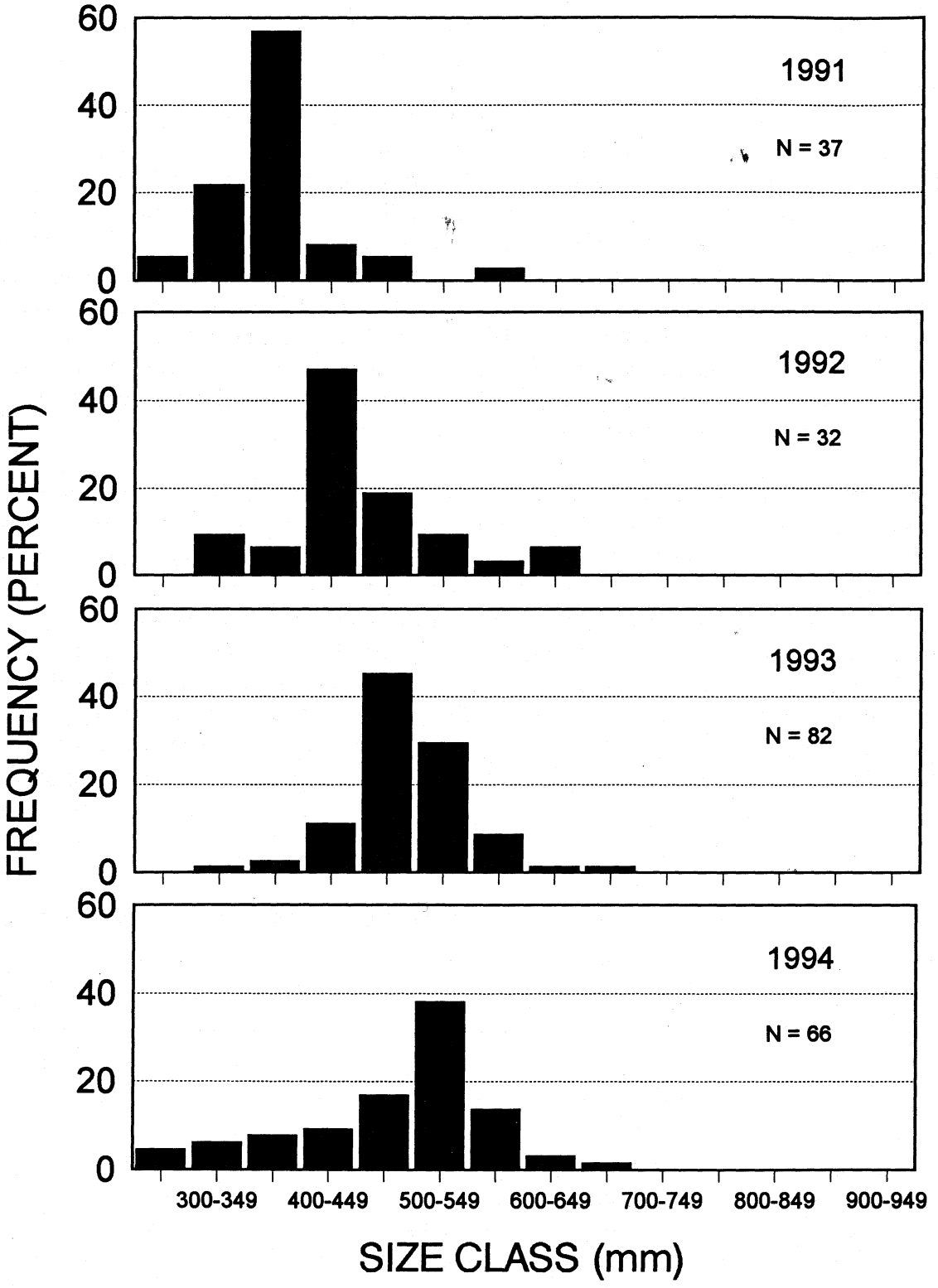


Figure 3. Length distributions of Colorado squawfish captured during 1991 through 1994 in the lower reach.

Their annual monitoring began in 1986; through 1990, average annual catch rates ranged from 0.2 to 0.5 Colorado squawfish/hr of electrofishing. Their program covers only 29% of the lower reach and confines itself to shoreline sampling. They did not detect this large group of young fish until the fish evidently had time to thoroughly disperse. Their lower reach catch rate was 0.3 fish/hr in 1991; by 1992 it increased to 1.5 fish/hr. There was no such similar spike in numbers or bulge in the size distribution in their first year of sampling, 1986, indicating that no relatively strong year class was produced during the previous nine years (since at least 1977). Thus, this pulse of young fish was probably the largest in a minimum of eight years (1977-1985).

Upper River Reach

Comparisons among subreaches. Size distribution (combined 1991-1994 data) of upper-subreach fish was significantly different from that of middle-subreach fish ($P = 0.003$, K-S test) and that of lower-subreach fish ($P = 0.0002$, K-S test); size distributions of middle and lower subreach fish were not significantly different ($P = 0.11$, K-S test). These distributions are illustrated in Fig. 4.

Comparisons of earlier years with recent years. Only the size distribution from the 1974 through 1976 period was significantly different from those of recent years. In the lower subreach, the largest group of fish during the 1979 and 1991-1992 periods was the 500-549 mm length class (Fig. 5). Growth slows as squawfish get older and therefore fish remain in this size group and succeeding ones for longer periods of time than in the preceding size groups (see Osmundson et al. 1996). In addition, recruitment from lower reaches of the river is probably largely completed by the time Colorado squawfish become much larger than this. In succeeding size classes, fish become fewer in number as annual mortality takes its toll on adults. During the 1991-1992 period there appeared to be a greater proportion of fish in the 400-499 mm size range than during 1979, though this difference was not significant ($P = 0.25$, test of proportions). For the combined upper and middle subreaches (Fig. 6), there was no significant difference ($P = 0.18$, K-S test) in size distributions between the 1982 and combined 1991 and 1992 time periods. A significant difference ($P = 0.00001$, K-S test) was found between length distributions of 20 years ago (1974-1976 data) and those of recent years in the middle subreach (Fig. 7); the proportion of fish < 550 mm TL then was significantly greater ($P = 0.00001$, test of proportions) than in recent years. In fact, many of the fish at that time (35%) were < 450 mm TL; the proportion of fish < 450 mm TL in the middle subreach was also significantly higher ($P < 0.0002$, test of proportions) 20 years ago than in the recent time periods. The highest proportion of fish < 450 mm TL in recent years was 10% in the lower subreach during 1991-1992.

Comparisons among recent years. In the lower subreach, size distributions appeared to change between 1991-1992 and 1993-1994, but differences were not significant ($P = 0.80$, K-S test). As mentioned above, the 500-549-mm length class contained the highest proportion of fish in 1991-1992. By 1993-1994, the proportion of fish in the 450-499 mm size

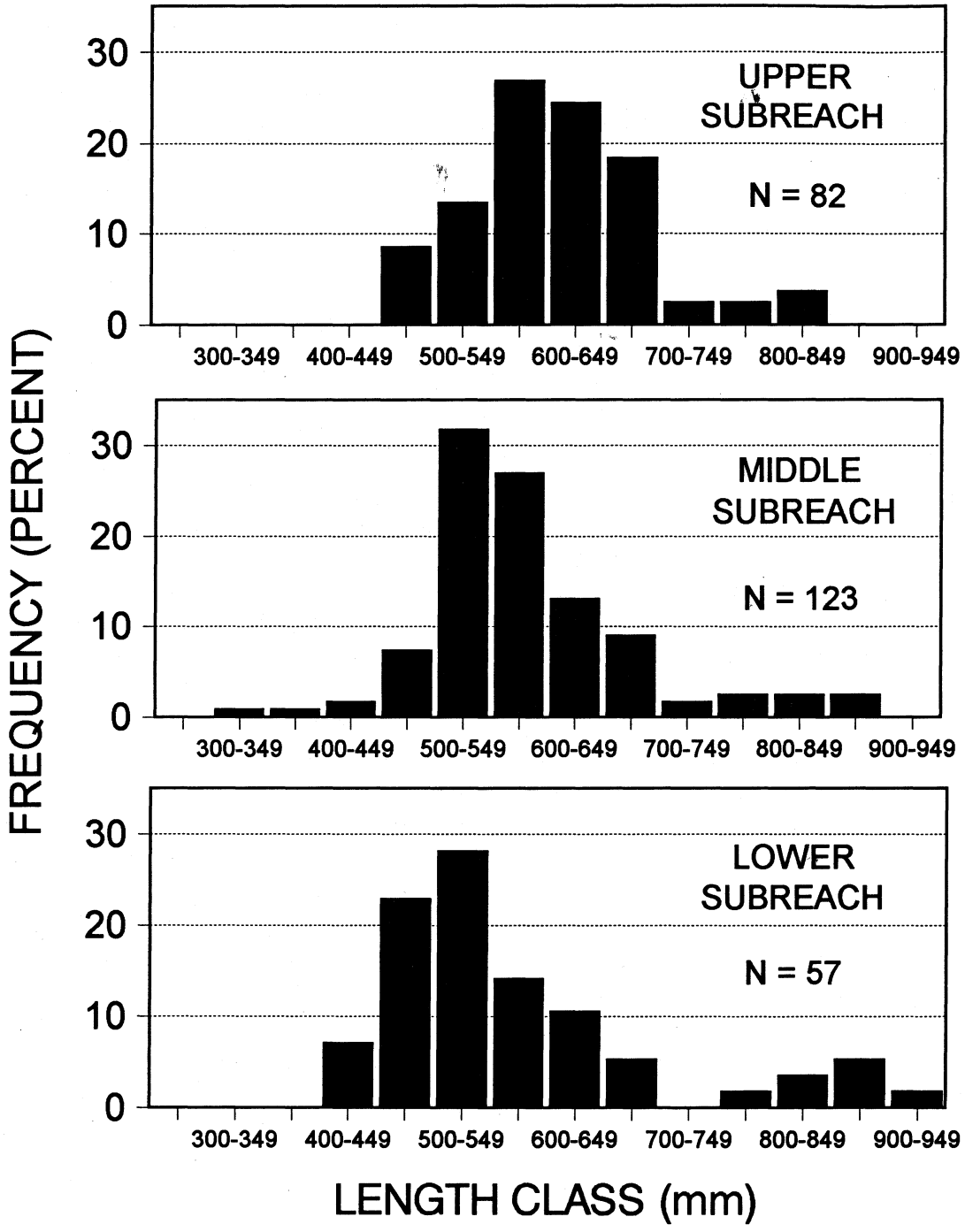


Figure 4. Upper-, middle-, and lower-subreach length distributions of Colorado squawfish captured during 1991 through 1994 (years pooled).

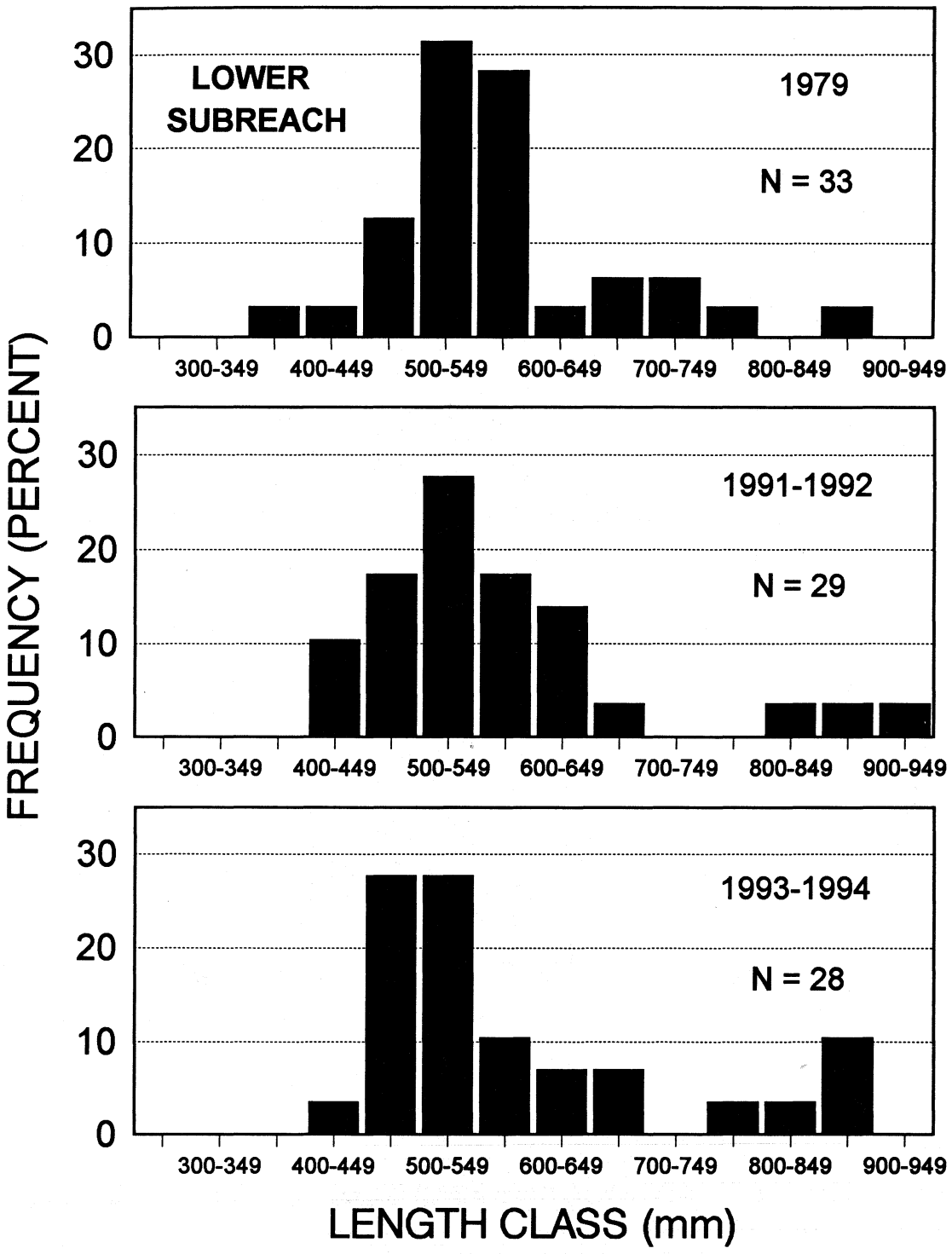


Figure 5. Lower-subreach length distributions of Colorado squawfish captured during 1979, 1991-1992, and 1993-1994.

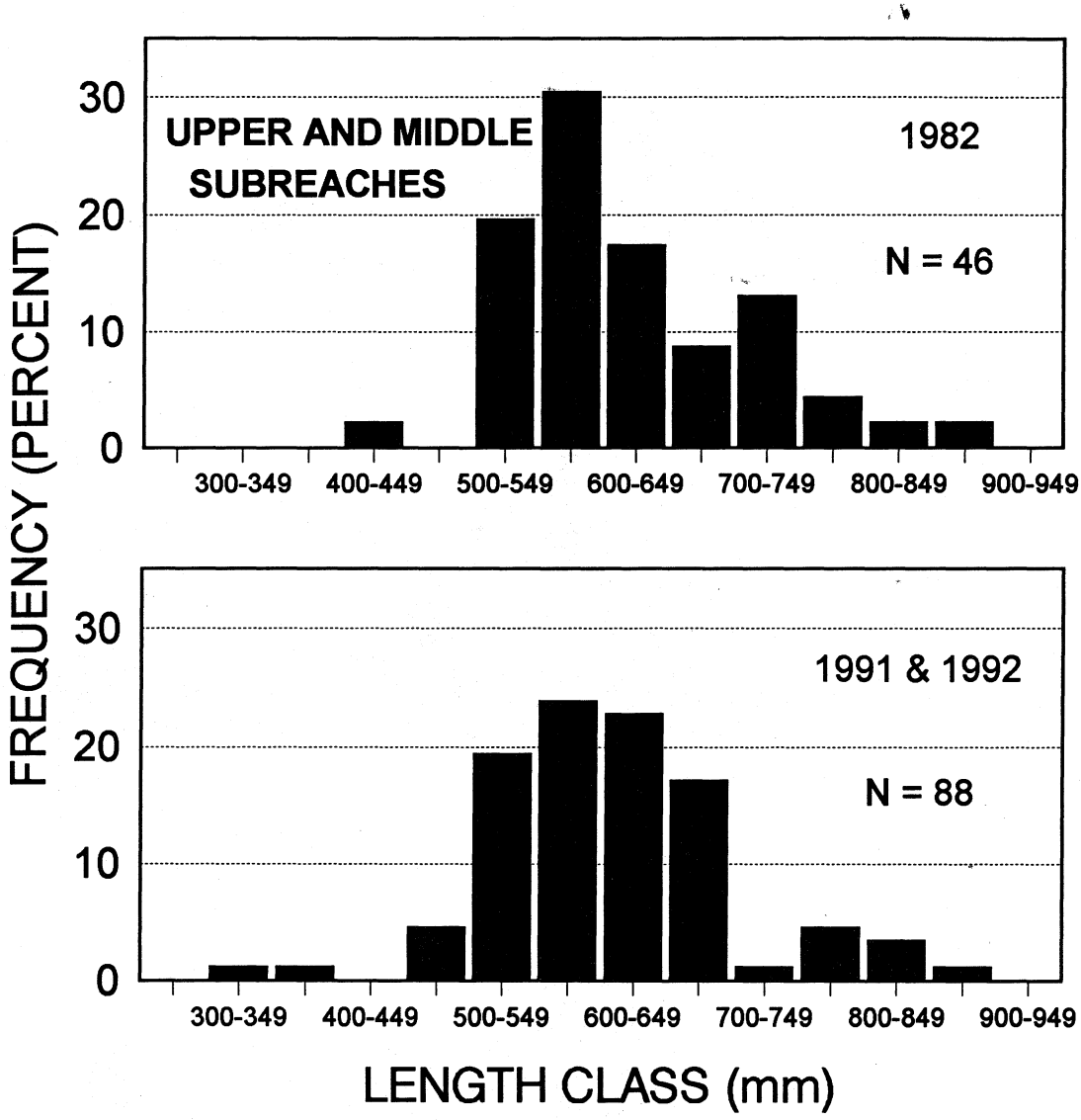


Figure 6. Upper- and middle-subreach (combined) length distributions of Colorado squawfish captured during 1982 and 1991-1992.

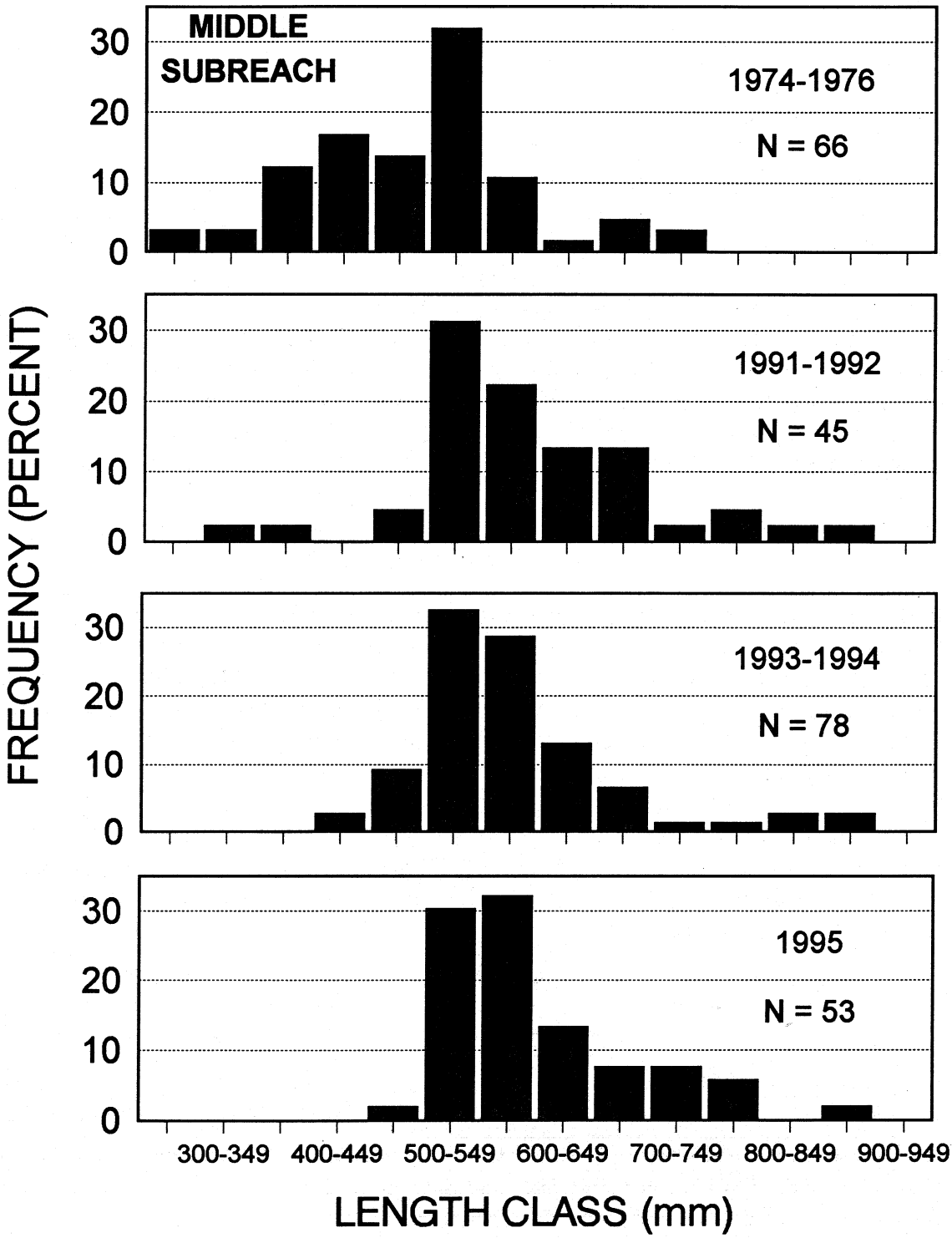


Figure 7. Middle-subreach length distributions of Colorado squawfish captured during 1974-1976, 1991-1992, 1993-1994, and 1995.

class apparently, though not significantly ($P = 0.34$, test of proportions), increased to become equal with the 500-549 mm size group, such that the bulk of the fish then fell within the 450-549 mm TL range (Fig. 5). This apparent shift in size distribution toward younger adults in the lower subreach was consistent with an expected migration from the lower reach of 1985-1987-year-class fish.

In the middle subreach, the highest proportion of fish was also the 500-549-mm-long group in 1991-1992 and 1993-1994, remaining at about 30% through 1995 (Fig. 7). Unlike the lower subreach, there was no major influx of 450-499-mm-long fish apparent during 1993-1994.

In the upper subreach, the 600-649-mm-length class was the most abundant group during 1991-1992. The size distribution then significantly changed ($P = 0.03$, K-S test), shifting to the left during 1993-1994; the most abundant fish became those in the 550-599-mm-long group (Fig. 8). In addition, the proportion of fish < 550 mm TL significantly increased ($P = 0.01$; test of proportions) during the two time periods. This also was consistent with the expected influx of young fish from the lower river.

Adult Catch Per Unit Effort

In the upper reach, mean CPUE of adults steadily increased from 1991 through 1994: 0.32 fish/net in 1991, 0.49 in 1992; 0.62 in 1993; 0.69 in 1994 (Table 7). Number of nets set per year was relatively constant ranging from 105 in 1994 to 139 in 1991. The lower subreach was least represented due to the low number of nettable backwaters there. When fish were partitioned by size it was apparent that the increase in CPUE was the result of increasing numbers of younger fish. Fish > 550 mm TL increased from 0.25 fish/net in 1991 to 0.33 fish/net in 1994; a difference that was not significant ($P = 0.59$). However, CPUE of fish < 550 mm long steadily increased from 0.07 fish/net in 1991 to 0.35 fish/net in 1994, a five-fold increase that was statistically significant ($P = 0.033$). Based on this data, Colorado squawfish < 550 mm TL made up approximately 22% of those netted in the upper reach during 1991; by 1994 they made up 51%.

Reproductive Success

Results from seining surveys indicated that 1986 and perhaps 1987 were comparatively good years for Colorado squawfish reproduction in the upper reach (Fig. 9). Mean CPUE of larvae was highest in 1986, but differences among years were not significant (df = 8, $X^2 = 9.24$, $P = 0.32$). Larvae were collected from the middle subreach (1-8 annually) during six of the nine years. All were collected downstream of RK 263.5. In 1986, one larva was also collected from the lower 3.5 km of the Gunnison River. No larvae or YOY were collected from the upper subreach during the study period, though one yearling-sized individual (105 mm TL) was captured there in 1986. YOY (1-29 annually) were captured from the middle subreach during six of the nine years; all were captured downstream of RK 262.7. CPUE was

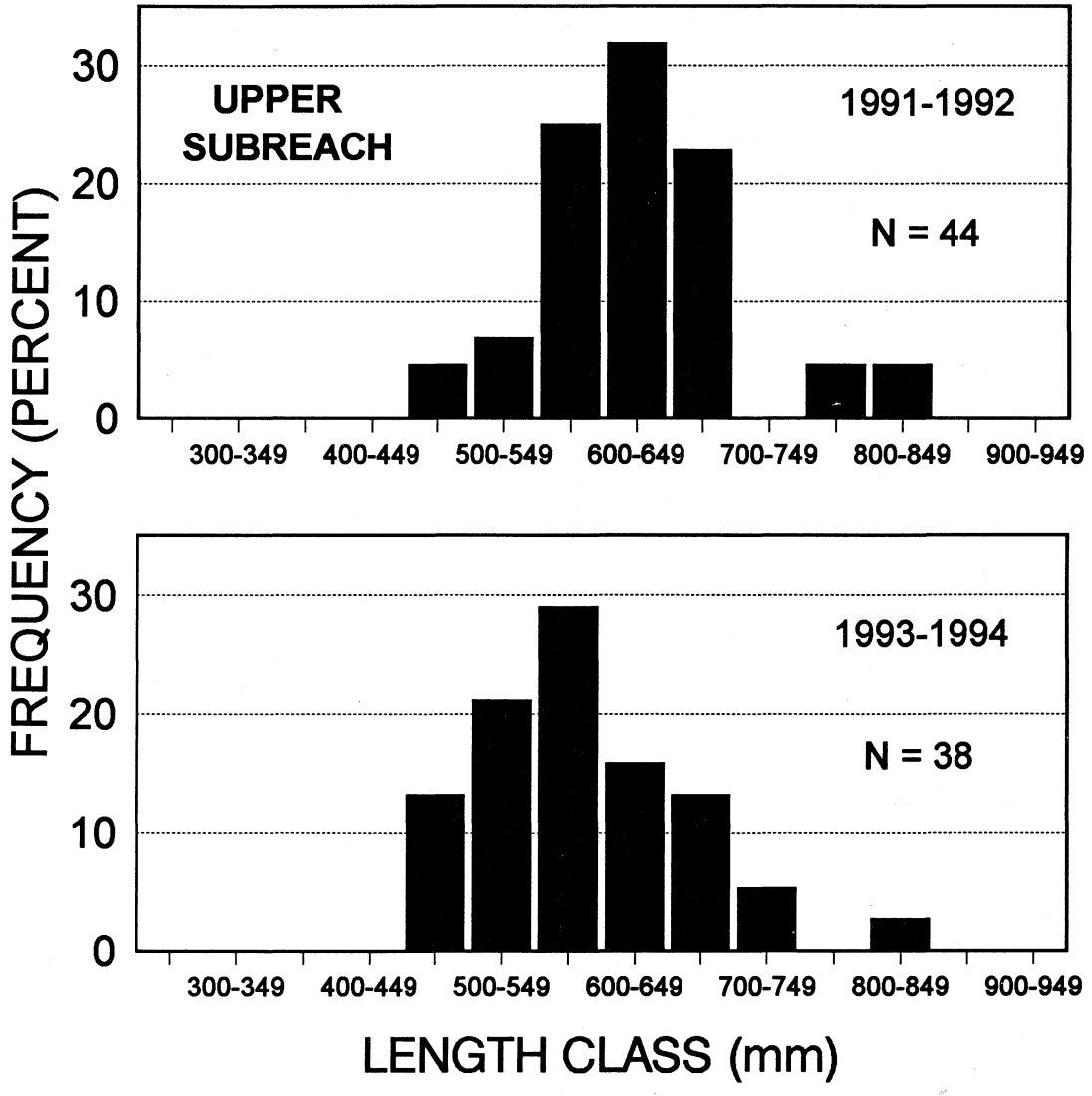


Figure 8. Upper-subreach length distributions of Colorado squawfish captured during 1991-1992 and 1993-1994.

Table 7. Mean catch per unit effort (CPUE) of Colorado squawfish captured in trammel nets (by year) in the upper reach (RK 200-298). CPUE = number of fish caught per net. N = number of nets set.

	All fish	< 550 mm TL	> 550 mm TL
		1991	
N	139		
Total fish	45	10	35
Mean CPUE	0.324	0.072	0.252
SE	0.065	0.022	0.061
		1992	
N	117		
Total fish	57	16	41
Mean CPUE	0.487	0.137	0.350
SE	0.086	0.036	0.074
		1993	
N	121		
Total fish	75	26	49
Mean CPUE	0.619	0.215	0.405
SE	0.112	0.053	0.082
		1994	
N	105		
Total fish	72	37	35
Mean CPUE	0.686	0.352	0.333
SE	0.142	0.094	0.075

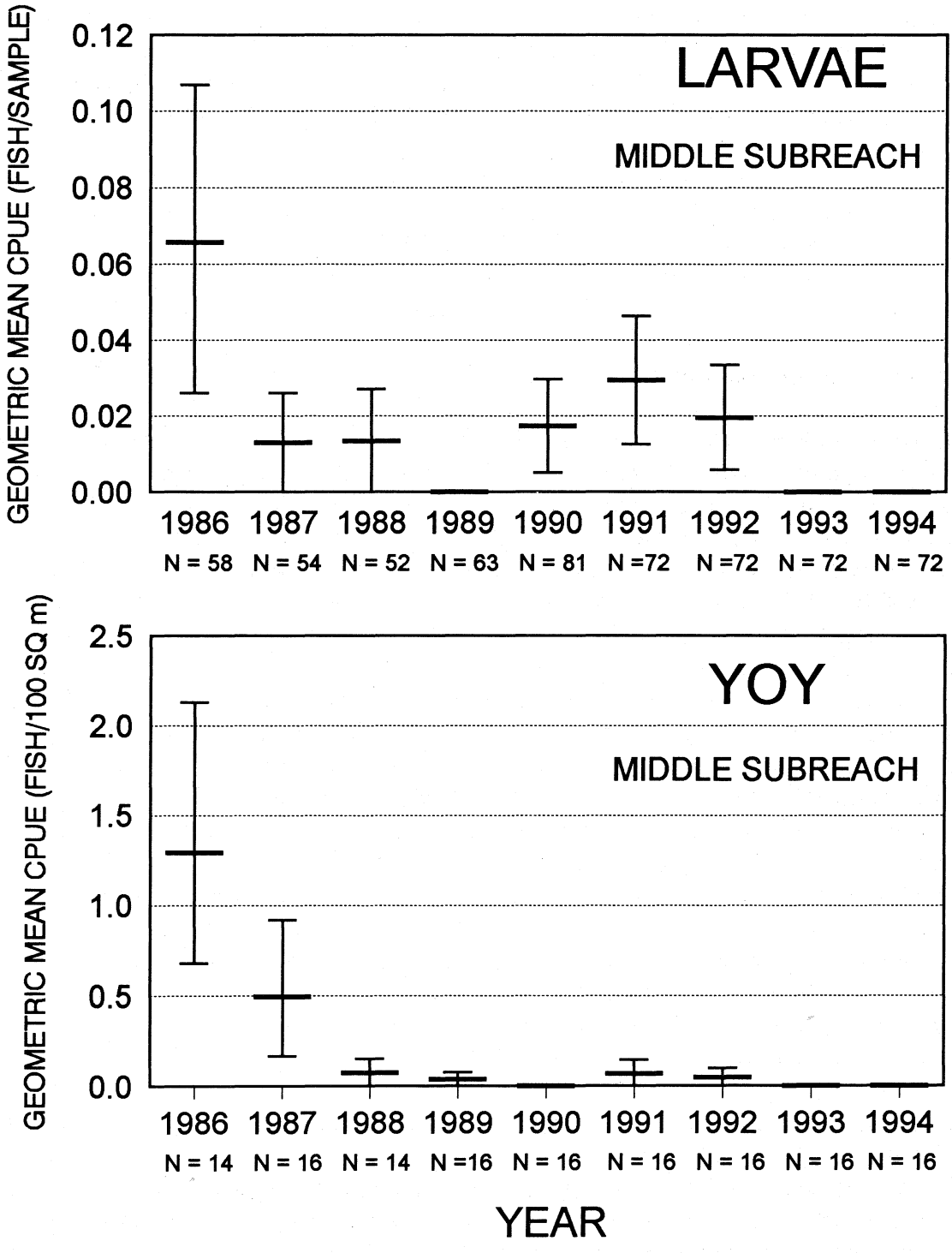


Figure 9. Annual catch-per-unit-effort of Colorado squawfish larvae (top) and young-of-the year (bottom) in the middle subreach during 1986 through 1994. Error bars are ± 1 SE.

significantly different among years (df = 8, $X^2 = 27.08$, $P < 0.0007$), with 1986 the only year significantly higher than others ($P < 0.05$). Though CPUE in 1987 appeared higher than in subsequent years, the difference was not significant ($P > 0.05$). Our results were similar to those of the ISMP for YOY in the lower reach: 1986 mean CPUE there was double that of any other year (McAda et al. 1994). In addition, earlier, river-wide, USFWS surveys of YOY extending back to 1982 indicated an even higher CPUE in 1985 than in 1986 (McAda and Kaeding 1989).

DISCUSSION

Status

Though some reproduction and recruitment no doubt occur in all years, strong year classes of Colorado squawfish are evidently infrequent. A distinct pulse of subadult fish was detected in the lower reach in 1991; within a few years these fish were distributed throughout the river. Based on aging a sample of these, this infusion of new fish into the population was evidently the result of one or more strong year classes produced during the mid-1980's. This was corroborated by catch rates of larvae and YOY during those years. Given that high reproductive success later resulted in strong recruitment, low numbers of adult Colorado squawfish in the Colorado River are likely the result of insufficient reproductive success during most years.

Degree of reproductive success is likely determined by environmental conditions that vary from year to year rather than by fluctuations in size of the spawning population, i.e., egg output. Apparent increases in adult numbers over the four years of this study did not result in concomitant increases in catch rates of larvae or YOY during the same time period. Conversely, weak year classes beginning in 1988 followed the relatively strong year classes of 1985 through 1987; although we have no data, there is no reason to suspect that there were significantly fewer adult spawners in 1988 than in 1986. Higher-than-average reproductive success during the mid-1980's may be related to the moderately high spring flows of this period following the exceptionally high flood years of 1983 and 1984. McAda and Kaeding (1989), Osmundson and Kaeding (1991) and McAda et al. (1994) found significant positive correlations between fall YOY catch rates in the Colorado River and the magnitude of spring flows that preceded the spawning season.

Our annual survival rate estimates of adult Colorado squawfish in the upper reach (0.84 and 0.86) were very similar to the survival rate estimated by Osmundson et al. (1996) for Colorado squawfish > 550 mm TL (0.86) using an entirely different approach. Though both methods used the same capture records, estimates here were based on capture-recapture histories whereas Osmundson et al. (1996) used a modified Chapman-Robson (Seber 1982) model where survival is based on declining numbers of increasingly older individuals.

Mortality rates must be balanced by recruitment rates to maintain long-term population stability . A long-term downward trend indicates that 1) recruitment has decreased, 2) mortality has increased, or 3) both 1 and 2 have occurred. Simulations can provide some idea of the sensitivity of this balance. For example, if a population starts with 250 adults with a 14% mortality rate (86% survival) and a 14% recruitment rate, and the survival rate is then increased to 90%, while keeping recruitment rate constant, it would only take 18 years for the population to double in size. A 4% increase in annual recruitment rate, while maintaining the current survival rate, would have the same effect. Because annual survival rate is probably fairly constant, our estimate likely reflects a long-term rate. Recruitment rate, however, varies greatly among years due to the variable nature of year-class strength; therefore, short-term rates, such as those estimated in this study, likely do not reflect long-term average rates.

Trends

Comparisons with historical abundance are difficult because of the paucity of biological studies or surveys conducted prior to the 1970's. Jordan (1891) conducted surveys in the upper Colorado River Basin at the turn of the century and described Colorado squawfish as "generally common". Jordan and Evermann (1896) described abundance and distribution with the following passage: "Colorado Basin, very abundant in the river channels as far north as the base of the Rocky Mountains in Colorado (Uncompahgre River at Delta)." Quarterone (1993) interviewed long-time residents of Grand Junction, Colorado and other localities and compiled accounts and photographs of their observations and experiences relating to native Colorado River fish during early to mid-century. One resident of Palisade, Colorado, Lyndon Granat, recalled, "And we caught what we called white salmon, which is the squawfish. And they were prolific, we caught lots of them." During a follow-up interview by the lead author of the present report, Mr. Granat also recounted how he and his father caught "between 30 and 40" Colorado squawfish in one day from the pool beneath the Price Stub Dam in 1922. He fished the Colorado River up until the 1940's and recalled that numbers of Colorado squawfish noticeably dwindled between the early 1930's and the early 1940's. These historic accounts, along with our current abundance estimates, strongly suggest that the long-term population trend has been downward.

Because of natural fluctuations, the significance of short term trends is difficult to evaluate. Based on the stable if not increasing numbers of adult Colorado squawfish during our four-year period of study, one might conclude that the population is stable. However, a longer time frame must be considered when evaluating trends of long-lived species, especially one with such a long lag-time between hatching and recruitment to the adult population. Although the 1985-1987 year classes gave the adult population a much-needed boost in numbers, reproductive success since that time has not been encouraging. Indeed, during the eight years following 1987, reproductive success has been relatively low and there have been few new juveniles captured in the lower river reach.

It is difficult to discern population trends by comparing size distribution of young fish between discrete years. Size distribution of fish < 550 mm TL is dynamic; year-to-year changes are dependent on the strength or weakness of recent year-classes. Only large differences are instructive of trends; for example, the complete absence of young adults for many years would shift the age distribution to the right and older fish would make up an increasing proportion of the adult population; such lack of recruitment would portend the eminent doom of a population. Osmundson et al. (1996) determined that large adults (> 550 mm TL) have exhibited a stable age distribution since 1982. However, a stable age distribution can be misleading: it is possible for the proportions of size or age groups to remain relatively constant while the overall number of adults gradually declines. No data are available that would allow an estimate of population size 15-20 years ago. Hopefully, information provided here will provide a baseline for future studies to compare against.

Perhaps the best evidence of a short-term trend is the decrease in proportions of juveniles and subadults in the upper reach during the past 20 years. During the Seethaler (1978) study, Colorado squawfish < 450 mm TL made up a substantial proportion of the upper reach size groups; from 1979 through the present, these smaller sizes have been virtually absent. The rarity of individuals < 450 mm TL in the upper reach today, coupled with the stable length distribution of adults > 550 mm TL, suggests that upper reach recruitment continues but its source is almost exclusively colonization from the lower reach. In addition, most individuals evidently do not move to the upper reach until they have attained a length of > 450 mm. If this is so, then the large number of individuals < 450 mm TL during the 1974 through 1976 period were likely reared in the upper reach. We hypothesize two explanations for this change: 1) nursery habitat in the upper reach was formerly of higher quality and quantity than in later years such that a smaller proportion of larvae drifted to the lower reach, and 2) successful reproduction and or hatching success in the upper reach was formerly much greater than that today such that substantial numbers of larvae were retained there even though proportions drifting to the lower reach may have been similar to those in recent years.

Prospects for the Future

Extinction and metapopulation theories argue that stochastic fluctuations cause local extinctions. In most extinction models, mean birth and death rates are assumed to be equal in the long term. Such models indicate a decreasing probability of extinction with increasing population size. Thus, to prevent extinction, the goal is to achieve a minimum viable population size, i.e., one large enough to withstand stochastic fluctuations without being driven to extinction (see Soule 1986, Simberloff 1988). Population size of *Ptychocheilus lucius* in the Colorado River evidently fluctuates according to the strength of recent year classes. Whether recruitment and death rates are equal over the long term is unclear. Up until the recent increase of young adults, very few adult-sized fish were captured in the lower river reach. Thus, our average estimate of ≈ 250 adult fish in the upper river reach may represent the bulk of the breeding population of the entire river during most years. In isolation, this

census number would indicate an effective population size below Franklin's (1980) threshold of 500 for genetic survival and Belovsky's (1987) evolutionary threshold of several thousand. However, occasional crossing over of individuals from the Green River population would likely alleviate any gene flow problems (Gilpin 1993). Stochastic demographic fluctuations are thus a greater threat than are genetic considerations. Relatively low numbers of adults and very infrequent strong year classes make this population vulnerable to extinction over time. What that time frame might be and what might constitute a minimum viable population size for the Colorado River we leave to future demographic modelers.

Most population viability models attempting to quantify time to extinction are based only on demographics and assume stability of habitat conditions. In reality, for many imperiled species, the threat of deterministic habitat change is far greater than stochastic demographic variation (Caughley 1994, Harcourt 1995), i.e., the causes for initial population decline are often still acting and in many cases worsening. This is likely the case for Colorado squawfish in the Colorado River: more water depletions are planned, more non-native species will be introduced, either intentionally or not, and the flood plain will continue to constrict from construction of additional jetties and dikes. *Ptychocheilus lucius* is well equipped to persist through long periods of adverse conditions: individuals are capable of living 30-50 years (Osmundson et al. 1996) and few are required to produce mass quantities of eggs. Under pre-development conditions, their basin-wide distribution provided adequate colonization sources if drought or other conditions temporarily rendered one or more tributaries uninhabitable. Gilpin (1993) suggested that if the Colorado River population became extirpated today, it would likely be replaced via colonization from the Green River. Indeed, according to Thomas (1994) the new vogue in metapopulation theory argues that local extinctions are balanced by colonization, citing Gilpin and Hanski (1991) and Harrison (1994). Crossing over from the Green River to the Colorado River, though probably rare, does occur: in 1996, an individual doing so was documented for the first time (Bob Burdick and Tom Chart personal communication). Recolonization is therefore physically and behaviorly possible. However, as Thomas (1994) argued, in most natural systems a balance between extinction and colonization is unlikely, especially for endangered species. If extinction is caused by a deterministic response to unsuitable conditions, the local habitat is likely to remain unsuitable and so be unavailable for recolonization. For the Colorado River, recolonization by Green River Colorado squawfish might follow extinction, but establishment of a new self-sustaining population by colonists would be unlikely until limiting habitat conditions were first improved. The same logic applies to stocking hatchery-reared Colorado squawfish to reestablish extirpated populations.

It is currently unknown what variables control the relative success of annual reproduction. If spawning and hatching success are linked to conditions created by spring runoff, changes in runoff pattern in the Colorado River during the past half century may in part explain the decline of this population. For example, high flows during spring may be required to create fresh cobble bars for spawning (Harvey et al. 1993) and adequately cleanse fines from existing bars (Haynes et al. 1984, Reiser et al. 1989). Absence of fines from gravel-cobble substrates appears to be the common denominator for spawning site selection by both the northern

(*P. oregonensis*) and Colorado squawfish (Beamesderfer and Congleton 1982, Lamarra et al. 1985). High egg-hatching success may require some minimum depth of interstitial voids for protection of deposited eggs and creation of micro-currents among voids for successful egg incubation. High flows may also serve to dilute waterborne contaminants from agricultural and urban sources that may interfere with reproductive behavior or reduce egg viability (Woodward et al. 1985, Hamilton and Waddell 1994). Bottomlands adjacent to the river require high flows to provide seasonal connectivity with the channel; periodic bottomland flooding is critical for maintaining a floodplain river's biological productivity (Junk et al. 1989, Bayley 1991, Rasmussen 1996). High flushing flows also serve to reduce numbers of non-native minnows that now dominate backwater nursery habitats (McAda and Kaeding 1989, Osmundson and Kaeding 1991, Muth and Nesler 1993). Laboratory and field experiments have implicated the prolific red shiner (*Cyprinella lutrensis*) as predacious on Colorado squawfish larvae (Ruppert et al. 1993), and fathead minnow (*Pimephales promelas*) larvae as competitive with Colorado squawfish larvae (Beyers et al. 1994).

If reproductive success is in part dependent on moderately high spring flows, perhaps preceded by an occasional flushing flood event, the attenuation of spring flows due to upstream dams and trans-basin diversions may explain the relative infrequency of strong cohorts in recent times. Van Steeter (1996) found that flows in excess of about 10,000 cfs were required to initiate movement of coarse bed materials in the vicinity of our upper subreach study area; a threshold of about 22,000 cfs is required before widespread mobilization of the bed occurs. Such bed mobilization is required to reshape the channel, build spawning bars and winnow fine sediments from the cobble bed. The frequency of such threshold flows has been greatly reduced since the middle part of the century (Osmundson and Kaeding 1991, Van Steeter 1996). If maintenance of proper physical or biological conditions requires a flow regime more approximating the historical norm, a higher frequency of strong year classes may be difficult to attain without spring flow augmentation.

The Recovery Implementation Program, a joint effort between federal and state agencies as well as water users and environmentalists, aims to recover endangered fish species in the Colorado River Basin while simultaneously allowing for additional depletions of water. Recovery actions designed to benefit Colorado River fish have included reservoir releases that augment low flows during late summer and fall and construction of a fish ladder at the base of the Gunnison River. Both actions should serve to increase the carrying capacity of the Colorado River system for adult Colorado squawfish. Also planned are attempts to reduce numbers of riverine nonnative fish and the reconnection of selected floodplain sites currently diked from the river. Mechanically removing nonnatives and controlling their source, if feasible, should serve to increase the chances of survival of young Colorado squawfish. These are important elements of an overall recovery strategy. However, if population size of Colorado squawfish is largely determined by the frequency of strong year classes, and if year-class strength is largely determined by the degree of spawning and hatching success, as we believe, then recovery actions may first need to address factors that limit spawning and hatching success before other recovery actions can be truly effective.

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