THESIS

AGE AND GROWTH OF COLORADO SQUAWFISH FROM THE UPPER COLORADO RIVER BASIN, 1978-1990.

Submitted by:

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In partial fulfillment of the requirements

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY JOHN A. HAWKINS ENTITLED AGE AND GROWTH OF COLORADO SQUAWFISH FROM THE UPPER COLORADO RIVER BASIN, 1978-1990, BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

AGE AND GROWTH OF COLORADO SQUAWFISH FROM THE UPPER COLORADO RIVER BASIN, 1978-1990.

Tagging records were examined for 2176 Colorado squawfish *Ptychocheilus lucius* collected from the Colorado, Green, White, Yampa, and tributary rivers. Length-frequency distribution modal range was 500-600 mm total length. Weight-length relationships were established for fish from each of the four primary rivers. Relative condition was greatest in spring and fall and lowest in summer. A body-length to scale-radius relationship was developed from 336 Colorado squawfish scales. Scales were aged and length at previous annuli estimated using the Fraser-Lee method. First annulus was not observed and may not form on most Colorado squawfish due to small size of fish at first winter. After adjusting for the missing annulus, scales were suitable for ageing Colorado squawfish up to 10 years old. Older ages were obtained but not validated. Oldest fish was an 18-year-old from the Yampa River. Estimated ages up to 10 years were validated with two 10-year-old stocked Colorado squawfish aged correctly at recapture. Additional validation of older fish with tagged and recaptured fish was partially successful. Relative growth calculated from lengths at tagging and recapture was lower than growth calculated from scales, suggesting either a detrimental tag effect or inaccurate ages of older fish. Coefficients of the von Bertalanffy growth function were derived from back-calculated lengths at age.

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DEDICATION

In memory of my grandfathers, Arnold Jeter Fuquay and John Hill Hawkins, Sr. They instilled in me a love of nature, an inquisitiveness for how things work, and provided me with loving parents, John and Darrell.

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INTRODUCTION

Colorado squawfish *Ptychocheilus lucius* historically inhabited the mainstream Colorado River and its tributaries downstream to the Gulf of California. Naturally occurring populations of the species are now confined to the Upper Colorado River Basin above Glen Canyon Dam. Upstream movements of the species are further restricted by barrier dams including Price-Stubb Dam on the Colorado River, Flaming Gorge Dam on the Green River, Redlands Dam on the Gunnison River, Navajo Dam on the San Juan River, and Taylor Draw Dam on the White River. The Yampa River is the only primary tributary that remains free-flowing within the native range of Colorado squawfish. Ancillary impacts downstream of these dams include water depletions, leveling of seasonal variation in the natural hydrograph, increased variation of daily flows from power generation, hypolimnetic cold-water releases, decreased sediment transport, and modification of downstream habitat (Miller 1961; Carlson and Muth 1989). The fishes of the basin are also affected by decreased water quality from agricultural, industrial, mining, and municipal pollutants; introduction of exotic fishes and vegetation; and poisonings to remove native "rough fish" populations (Ellis 1914; Miller 1961; Carlson and Muth 1989). These cumulative and synergistic impacts caused the decline of Colorado squawfish. The species was identified as in danger of extinction by the United States Fish and Wildlife Service (USFWS) and is protected by the Endangered Species Act of 1973.

The Endangered Species Act, in part, requires a recovery plan to stop and reverse the decline of each endangered species. Recovery means restoration of each population to a size that is no longer in danger of extinction and able to naturally reproduce self-sustaining numbers. To document recovery, we need to know population size, natality, mortality, and age and growth parameters of the species. Fishery texts identify the importance of this information in managing a fishery (Ricker 1975b; Everhart and Youngs 1981; Jearld 1983). Recruitment, growth, and mortality rates are the three most important population rate functions necessary for proper management of a fishery (Summerfelt 1987). The emerging discipline of conservation biology has emphasized use of scientific information to manage non-game species such as Colorado squawfish. We may never know the former abundance or distribution of Colorado squawfish, but we must identify current population parameters in order to manage its future.

Knowing the age of a Colorado squawfish when it undergoes a specific activity increases our understanding of life-history events. Important ages are age of sexual maturity, age at migration, maximum age, and ages of different habitat use. Age composition which shows the relative percentage of each age group within a population, is useful for determining population structure and mortality. Age data when combined with fish length can be used to calculate growth. Although constrained by genetic limits, growth is influenced by environmental factors such as temperature, photoperiod, habitat, competition, and food. Identifying the growth rate of individuals in a population can help biologists identify genetic or environmental factors that enhance or impede growth.

Length and weight data can also characterize a population. A length-frequency distribution, the number fish collected in each size group, can identify recruitment and show abundant or lacking sizes. The relationship of weight to length can be either descriptive or predictive. The mathematical relationship can be used to convert one measure to the other, usually by calculating the expected or average weight at a given length. The equation describing the relationship can be used to differentiate populations, subgroups, or other smaller taxonomic units (Le Cren 1951). This relationship can also be used to calculate fish condition, which is often interpreted as an indicator of individual or population well-being (Tesch 1968; Bolger and Connolly 1989).

Humans are naturally curious about animals that are either large or old. This interest is illustrated by the tendency of many authors to characterize Colorado squawfish as North America's largest minnow (e.g., Ellis 1914; Miller 1955; Haynes et al. 1984; Tyus 1990). Ellis (1914) and Miller (1955) suggested a historical maximum length of 1.8 m and weight of 45 kg for Colorado squawfish in the lower Colorado River. Early explorers in the 1800s reported angling Colorado River salmon (Colorado squawfish) that ranged 760-910 mm long (Dellenbaugh 1962). Photographs from the early 1900s in Vanicek (1967), Minckley (1973), and Seethaler (1978), support the historical occurrence of large Colorado squawfish. Whether these large fish were common in the past remains unknown, but few fish over 800 mm long have been collected in the last 25 years. Behnke and Benson (1983) suggested that declines of large forage fish such as bonytail *Gila elegans* may have led to a decline of large Colorado squawfish. Kaeding and Osmundson (1988) attributed slow growth of Colorado squawfish in the Upper Colorado River Basin to sub-optimal water temperatures that are historic to these upper reaches.

Previous studies

Several previous studies of Colorado squawfish growth have focused on either early life stages or hatchery stocks. Tyus and Haines (1991) examined over-winter growth of wild, age-0 Colorado squawfish seined from the Green and Yampa rivers from 1979 to 1988. Fish were generally larger in the spring (mean, 45 mm) than the previous autumn (mean, 42 mm). The size difference was attributed to either growth or size-selective mortality. Black and Bulkley (1985b) examined the relationship between growth rate of hatchery-raised yearling Colorado squawfish and four different temperatures (15, 20, 25, and 30°C). Maximum growth occurred at 25°C, which was also identified as the preferred temperature of yearling Colorado squawfish (Black and Bulkley 1985a).

Osmundson (1987) studied growth and survival of young Colorado squawfish in riverside ponds along the Colorado River. Growth rate of age-1 Colorado squawfish raised in ponds was twice that reported by Seethaler (1978) for fish from the mainstream Colorado River. Additional study under similar conditions by Osmundson and Kaeding (1989) also revealed growth rates higher in fish from ponds than from the mainstream, but not as high as the rate originally reported by Osmundson (1987). This exceptional growth was attributed to abundant forage and warmer temperatures available in pond environments.

Three previous studies were conducted on age or growth of wild Colorado squawfish. These include part of a dissertation (Vanicek 1967) that was later published (Vanicek and Kramer 1969), part of a master's thesis (Seethaler 1978), and a mimeographed report (Musker 1981) to the USFWS. Vanicek (1967) performed the first age and growth study on Colorado squawfish collected from the Yampa and Green rivers within Dinosaur National Monument during 1964-1966. He used scales to age 167 fish and back-calculated average length and growth per group. Ages estimated from scales were validated by 1) comparison and agreement with length-frequency distributions of age-0 to age-2 fish and 2) agreement with calculated lengths of fish collected in different years. Vanicek (1967) noted a decrease in average growth rates of Colorado squawfish from 1958 to 1965, based on average growth obtained from back-calculation. No important differences in growth or year-class strength were noted between years with different flow regimes. Larger, older fish were not well represented; only 38 adults were aged. Age validation was limited to age groups less than 2 years old, and older ages were not validated.

Seethaler (1978) aged scales from 68 Colorado squawfish from the Colorado River and 63 from the Green and Yampa rivers. Fish were collected during 1974-1976. Seethaler (1978) compared these data with those of Vanicek (1967) and determined that fish grew faster in 1974 to 1976 than in 1964 to 1966. Growth rates were apparently equal between 1974-1976 but differed between the Colorado River and the Green and Yampa rivers. Seethaler (1978) was unable to detect the first annulus on Colorado squawfish scales and adjusted his age data accordingly. Validation methods were not discussed. Size at sexual maturity was determined by necropsy of 147 Colorado squawfish from the University of Utah fish collection.

Musker (1981) aged scales from 152 Colorado squawfish collected from the Colorado (14), Green (103), Yampa (26), and White (9) rivers between 1979 and 1981. Fin-ray sections from two fish were used to corroborate ages determined from scales. Musker calculated a body-length to scale-radius relationship for fish from each river, but due to small sample sizes and lack of small fish, these relationships were probably not accurate. These inaccuracies affected the back-calculation of estimated fish lengths at earlier annuli. Musker also did not account for the missing first annulus, thus under-ageing fish by at least 1 year. If the missing annulus is included, Musker's ages were probably accurate, but his back-calculated lengths at earlier ages are suspect.

Objectives

The objectives of my study were as follows.

1) Evaluate use of scales as an accurate ageing method for Colorado squawfish.
2) Validate scale ages with fish of known age and with mark-recapture information.
3) Determine average individual growth rates and compare between populations.
4) Determine age composition of each sampled population.
5) Characterize each sampled population by length-frequency and length-weight relationships.
6) Calculate monthly condition of fish from each sampled population.

METHODS

This study contains two types of data. Tagging records of Colorado squawfish collected from the Upper Colorado River Basin were used for length and weight analyses and to calculate growth. The other data type was from scales taken from Colorado squawfish collected in studies by Colorado State University Larval Fish Laboratory, and Colorado Division of Wildlife. Additional scales were obtained from fish collected by other state and federal agencies and private consultants. Scales were used to estimate ages and growth history of individual Colorado squawfish.

Capture and tagging records

Some records of Colorado squawfish tagged from 1978 through 1989 were obtained from the database administrator of the USFWS, Grand Junction, Colorado, field station. Additional records were obtained from agency progress reports and personal communication with researchers. Agencies involved in these collections included Bio/West, Inc.; Colorado Division of Wildlife; Colorado State University; New Mexico Department of Fish and Game; New Mexico State University; Utah Department of Natural Resources; and USFWS field stations in Grand Junction, Colorado, and Vernal, Utah. Other records of Colorado squawfish tagged between 1978 and 1989 probably exist but were not obtainable. Colorado squawfish that were collected but not tagged were not included in this study because their records were not well documented. Tagging records were combined from the different sources, checked for errors, and assembled into a consolidated database. Several errors were encountered in these records. These problems and recommendations concerning this database were discussed by Hawkins (1991).

Tagging records represented Colorado squawfish collected from the Colorado, Duchesne, Green, Gunnison, Little Snake, Price, San Juan, White, and Yampa rivers. Gear types included angling, electrofishing, fyke nets, gill nets, trammel nets, and seines. Information documented at capture included river-mile location, habitat identification, and fish length and weight measurements. Colorado squawfish over 200 mm total length (TL) were tagged under the dorsal fin with either Floy anchor or Carlin dangler tags. Length of each fish was measured to the nearest mm using a standard measuring board with a fixed headpiece (Anderson and Gutreuter 1983). Total length was measured from anterior margin of snout to tip of the longest caudal fin ray with caudal fin compressed dorso-ventrally (Anderson and Gutreuter 1983). Weights were measured with balance or hanging scales of varying type and capacity. Sex was determined by the expression of gametes, although it was sometimes based on secondary sexual characteristics.

Tagging records were used for analyses of length-frequency distribution and weight-length relationship; tag-recapture records were used to calculate growth. For most analyses, capture records were stratified by river of capture. Records from smaller tributaries from which few fish were captured were added to records of each mainstem river. Fish were stratified by river because adult Colorado squawfish establish and maintain residency in specific river reaches; such groups should be considered separate stocks (Wick et al. 1983; Tyus 1990). This does not imply reproductively isolated populations. Colorado squawfish that over-winter together in the same river reach may migrate to different spawning locations (Tyus 1990). A fish collected from the Yampa River spawning area could have come from an over-winter area on either the Green River or Yampa River. A capture record of this fish would be grouped with other fish collected from the same river.

Fish were further stratified by month of capture because water temperature and food availability vary with season. This variation would affect growth and condition. Few immature fish were tagged in this study, so only mature fish were used for developing weight-length relationships and calculating condition. Mature fish were defined as fish over 428 mm TL. Vanicek and Kramer (1969) found that nearly all fish older than age 7 (estimated length 454 mm) were sexually mature. Seethaler (1978) necropsied 147 Colorado squawfish between 184 to 652 mm TL. He found that all fish longer than 503 mm TL were sexually mature, and fish less than 428 mm TL were immature. Of the 34 fish he examined between 428 to 503 mm TL, 76% were mature.

Many fishes exhibit sexual dimorphism after maturity and are usually stratified by sex when calculating weight-length relationships, condition, or growth rates. Colorado squawfish were difficult to sex by external characteristics, so few fish were identified as male or female. Fish were not segregated by sex during analyses.

Weight-length relationship

The weight-length relationship for most fish is described by the power function:

$$W = aL^b, \tag{1}$$

where W equals weight, L equals length, and a and b are constants. If b equals 3, growth is isometric and shape does not change as length increases. If b does not equal 3, growth is allometric and shape changes with an increase in length. When b is less than 3, fish become less rotund as length increases. Generally, b is greater than 3, indicating that fish become more rotund as length increases (Anderson and Gutreuter 1983). The constants a and b are estimated by logarithmic transformation of equation (1). Then,

$$\log_{10} W = \log_{10} a + b \log_{10} L, \tag{2}$$

where $\log_{10} a$ is the intercept, and b is the slope of the line. These constants are estimated by either least-squares (ordinary major axis) or geometric-mean (standard major axis) regression. The geometric-mean method is often recommended because weight is not truly independent of length, and both are subject to errors or fluctuations (Ricker 1973, 1975a, 1975b; Anderson and Gutreuter 1983; Bolger and Connolly 1989), but this method has been considered inappropriate and difficult to interpret (Sprent and Dolby 1980; Cone 1989). Least-squares regression is commonly used due to its "better understood" statistical properties (Jolicoeur 1975; Bolger and Connolly 1989). An excellent review of methods for determining the weight-length relationship was provided by Le Cren (1951).

The regression equation of weight and length provides a good description of a population or subgroup, but a valid comparison between groups is difficult because two parameters (*a* and *b*) must be considered (Bolger and Connolly 1989). Often, only slopes are compared, with larger slopes indicating faster growth and therefore better condition, but slopes should be compared only when intercepts are equal (Bolger and Connolly 1989). If slopes of different subgroups are equal, as determined by analysis of covariance, intercepts are good indicators of the condition of each group (Le Cren 1951; Bolger and Connolly 1989). An analysis of co-variance between months was performed on regression equations using SAS statistical packages (SAS Institute, Cary, N.C.) for micro-computer. Slopes and y-intercepts from each weight-length regression equation were compared between months of capture for each river.

Fish condition

A condition index provides an indication of fatness, well-being, or gonad development of a fish (Le Cren 1951). Condition measures the variation between actual fish weight and expected weight. Condition factor is derived by rearranging equation (1) into:

$$c = \frac{W}{L^b}, \qquad (3)$$

where c is equivalent to a in equation (1). Fulton's condition factor (K) is often used:

$$K = \frac{W}{L^3} * 10^n, \qquad (4)$$

where n equals 2, 3, 4, or 5, depending on units of measure. The asterisk (*) signifies multiplication. The scaling constant (n) converts K to a mixed number for better comprehension (Anderson and Gutreuter 1983; Cone 1989). Fulton's K represents growth of an idealized fish with isometric growth where weight is proportional to length cubed. Although K is easy to calculate and does not require knowledge of the weight-length relationship it has several problems. The value of K will vary for the same fish depending on whether metric or English measurements are used (Anderson and Gutreuter 1983). It assumes that growth is isometric (b=3). Fish of different lengths cannot be compared because K increases with length if b for the population is greater than 3. Anderson and Gutreuter (1983) suggested limiting comparisons to similar lengths. Cone (1989) cautioned that each stratum (e.g., sex, strain, growth stanza) to be compared should be checked to confirm isometric growth.

Although used regularly, Fulton's condition factor has been deemed inappropriate because it does not account for allometric growth and because fish of different sizes were to be compared. Instead, relative condition (*Kn*) was calculated for individual fish from each river with the formula:

$$Kn = \frac{W}{aL^{b}} * 100, \quad (5)$$

where *a* and *b* are constants from the weight-length relationship. This equation is similar to relative condition (*Kn*) described by Le Cren (1951), and relative weight (*Wr*), which Wege and Anderson (1978) calculated by pooling data from several different fish populations in North America. For valid comparison, slopes and intercepts of any populations to be compared must be equal to those of the ideal population. Cone (1989) illustrated how different slopes or intercepts would adversely affect the outcome of *Wr* (or *Kn*) calculation. Relative condition provided a simpler statistic for comparison than *a* or *b* from the weight-length equation (2). The resulting *Kn* is comparable between fish of different lengths or species, and it does not change with different units of measurement (Le Cren 1951). Average fish of any species or length will have a *Kn* of 100. Properties and associated problems of condition factors were discussed in detail by Le Cren (1951), Bolger and Connolly (1989), and Cone (1989). A *Kn* was calculated for each fish collected from each river.

Each *Kn* value represented the deviation of a fish from the expected mean weight for a given length of all fish in its own group. Fish were grouped by month of capture from each river. Values of expected weight were derived from the pooled weight-length regressions for each river. Only mature fish (> 428 mm TL) were used in the calculations because tag records of immature fish were limited. Individual values of *Kn* were averaged to estimate the condition of fish during each month.

Age and growth

Scales were taken from tagged Colorado squawfish collected between 1979 and 1989 and from small untagged fish collected from the Green River in 1990. Scales were removed between the lateral line and insertion of the dorsal fin. Scale samples were placed between wax paper within small envelopes labeled with collection date, river and river mile of capture, species, sex, Carlin tag number, fish TL (mm), fish weight (g), and if the fish was a recapture.

Scales were soaked in water and cleaned with a soft artist's brush. Each scale sample was mounted wet between microscope slides, which were taped closed, and dried. Species, tag number, and capture date were recorded on each slide. Scales were magnified 39 times original size with a Bausch and Lomb micro projector. Each scale image was projected onto a sheet of paper that contained orientation axes (Figure 1). The anterior portion of the scale was

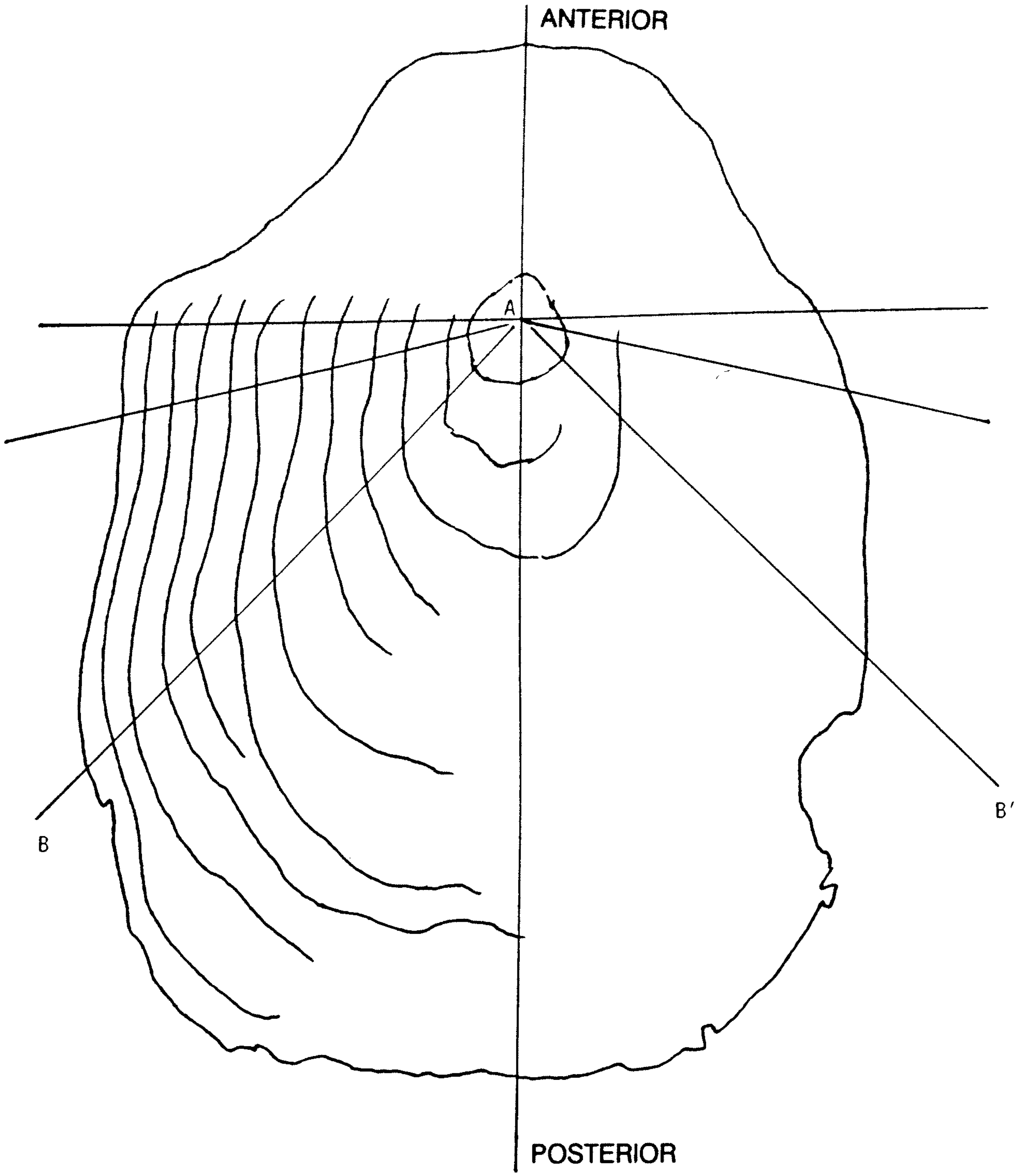

Figure 1. Orientation of scale tracing along several axes and location of annuli measurements (line A-B).

oriented to the top of the sheet, and the scale focus was transected by the axes. Scale margin and annuli were traced onto the paper as a record for each scale. Measurements for back-calculation were made along a posterior radius of the scale at either line A-B or A-B' (Figure 1).

Scale tracings were measured from the focus to each annulus and to the scale margin. Total length was plotted as a function of scale radius, and a line was fitted with least-squares linear regression of the form:

$$L = a + b * SR, \qquad (6)$$

where L is fish length (mm), SR is scale radius (mm), b is the slope, and a is the y-intercept of the line. The intercept (a) estimates fish length at scale formation (Tesch 1968). However, Carlander (1969) warned that this may not always be true because early scale growth is not proportional to later growth of the fish.

Back-calculation of length

Estimated total length at each annulus (L_i) was back-calculated by the Fraser-Lee method using equation:

$$L_i = \frac{(L_c - a)}{S_c} * S_i + a, \qquad (7)$$

where L_c is fish total length (mm) at capture, S_i is scale radius at the i^{th} annulus, S_c is scale radius at capture, and a is the intercept from equation (6). Total lengths were calculated for all annuli from each fish and averaged by age group in a summary table. The computer program DISBCAL was used to calculate the fish-length to scale-radius regression and back-calculate length at each annulus (Fry 1982; Anonymous 1989).

Age validation

Ages were validated by known-age, hatchery-reared fish that were released into the wild and later recaptured. Additional validation came from ageing tagged fish that were later recaptured. The known time interval between tagging and recapture was compared to the estimated time interval between tagging and recapture. Estimated time interval was obtained by subtracting estimated age at recapture from estimated age at initial tagging. These two methods are the only recognized techniques to validate estimated ages for older fish (Beamish and McFarlane 1983).

Relative growth

Relative growth was calculated from recaptured fish for comparison with increments derived from back-calculated lengths. Average yearly growth was calculated for tagged and recaptured Colorado squawfish. Recaptured fish were often at large during colder months when growth would be negligible. The period of potential growth was based on water temperatures. Black and Bulkley (1985a) found that growth at 15°C was only 18% of the rate achievable at the preferred temperature of 25°C. Kaeding and Osmundson (1988) evaluated data from Black and Bulkley (1985a) and determined that growth of

Colorado squawfish ceased at temperatures below 13°C. April through September were considered potential growth months because they have water temperatures above 13°C. This corresponded with the 6-month growth period identified by Kaeding and Osmundson (1988). Although mainstream river temperatures may not be above 13°C in April, temperatures in shallow backwaters often surpass this temperature in April or May. Adult Colorado squawfish often use warmer backwaters in the spring (Wick et al. 1983). Only days within the potential growth period (April 1 - September 30) were counted in the interval between tagging and recapture. A fish tagged August 1 and recaptured the following May 1 would have spent 240 days between captures; but the growth interval would have been only 90 days (i.e., 30 days in August + 30 days in September + 30 days in April).

Recaptured fish were classified into one of three categories: those recaptured less than 1 year later, those recaptured approximately 1 year later, or those recaptured more than 1 year later. Growth from each period was converted to average yearly growth increment. Fish recaptured less than 30 days after tagging were not included in the analysis because a small measurement error could be magnified dramatically when converted to yearly growth. Negative growth of individual fish was converted to zero growth prior to calculation of length-group averages. Relative growth was calculated by dividing the increment grown during a year by initial length at the start of that year.

von Bertalanffy growth function

Average lengths at age from the scale back-calculation summary table were used to estimate three unknown parameters (L_∞, K, and t_0) of the von Bertalanffy growth equation:

$$l_t = L_\infty (1 - e^{-K(t - t_0)}), \tag{8}$$

where l_t is length at time t, L_∞ is asymptotic length, e is the base of natural logarithms, K is a growth coefficient, and t_0 is the time when length would theoretically be zero.

Methods of estimating the unknown parameters follow those outlined by Everhart and Youngs (1981). Mean length at age $t + 1$ (i.e., $l_t + 1$) was plotted as a function of mean length at age t (l_t) on a Walford plot (Walford 1946). A linear regression was fitted by the least-squares method. Asymptotic length (L_∞) was estimated as the point where ($l_t + 1$) is equal to l_t. Solving the linear regression equation of the Walford line for y=x or ($l_t + 1$) = l_t results in an estimate of L_∞:

$$L_\infty = \frac{a}{1 - b}, \tag{9}$$

where a is the y-intercept, and b is the slope from the Walford-plot regression. To obtain an estimate of K, the von Bertalanffy growth curve (equation 8) was transformed to:

$$\log_e (L_\infty - l_t) = \log_e L_\infty + Kt_o - Kt. \tag{10}$$

This is similar to the linear equation:

$$y = a + bx, \tag{11}$$

by substitution, y equals $\log_e (L_\infty - l_t)$, a equals $\log_e L_\infty + Kt_o$, b equals $-K$, and x equals t.

By plotting $\log_e (L_\infty - l_t)$ as a function of t and fitting a regression line, an estimate of t_o can be obtained from the equation:

$$t_o = \frac{a - \log_e L_\infty}{K}, \qquad (12)$$

where a is the intercept, K is the negative slope of equation 10, and L_∞ is from equation 9.

The parameters L_∞, K, and t_o used in the von Bertalanffy growth curve (equation 7) were estimated for fish from the Colorado, Green, White, and Yampa rivers. Data from back-calculation tables from previous studies were also used to estimate von Bertalanffy growth parameters of fish from the Green River, and length at age was compared with lengths from this study.

RESULTS AND DISCUSSION

Capture and tagging records

Records of tagged or recaptured Colorado squawfish during the 12-year period, 1978-1989, totaled 2176. Most records were from the Colorado (422), Green (1086), White (146), and Yampa (465) rivers (Table 1). Price River (n=1) and Duchesne River (n=20) records were combined with those from the Green River, the Little Snake River (n=1) was combined with the Yampa River, and the Gunnison River (n=27) was combined with the Colorado River. Fish were captured from March through November, but numbers caught varied among months due to greater sampling effort or vulnerability in some months. Of the tagged fish, 279 were recaptured at least once, 42 were recaptured twice, and three were recaptured three times.

Most Colorado squawfish sexed were males. Sex was identified for only 165 fish; 130 (79%) were males. This disproportionate number of males may be due to the methods used to identify sex. Males were more easily identified because they were ripe for a longer period than females. It was also easier to express gametes from males than from females. A few identifications were based on secondary sexual characteristics but were potentially inaccurate. For example, one fish (tag number 3136, tag color red) was identified as a male at

Table 1. Number of Colorado squawfish tagged or recaptured in the Upper Colorado River Basin, 1978-1989. NA = river or year of collection information was not available.

	River of capture										
	Yampa	Little Snake	Green	Colorado	White	Gunnison	Duchesne	San Juan	Price	NA	Total
1978	1	0	2	0	6	0	0	0	0	0	9
1979	15	0	35	55	2	7	0	0	0	0	114
1980	32	0	69	52	3	1	0	0	0	0	157
1981	71	0	79	30	55	4	0	0	0	0	239
1982	72	0	69	78	18	4	0	0	0	0	241
1983	40	0	94	43	11	0	0	0	0	0	188
1984	50	0	118	34	12	0	19	0	0	0	233
1985	60	0	220	48	24	0	0	0	1	0	353
1986	40	0	156	35	5	1	1	0	0	0	238
1987	45	0	132	21	3	9	0	4	0	0	214
1988	35	1	106	24	7	1	0	3	0	0	177
1989	4	0	6	2	0	0	0	0	0	0	12
NA	0	0	0	0	0	0	0	0	0	1	1
Total	465	1	1086	422	146	27	20	7	1	1	2176

capture and a female at recapture (Hawkins 1991). Tagging records did not identify which methods were used to identify sex.

This sex ratio may accurately reflect the true sex ratio for the species. Seethaler (1978) sexed 147 fish by necropsy and identified a similar proportion (83%) as males. Colorado squawfish, a broadcast spawner would be expected to have more males than females.

Length-frequency distributions

Total length of tagged Colorado squawfish from all rivers averaged 536 mm with a range of 81-896 mm. The modal length group was 500-550 mm for fish from the four primary rivers. Mean total lengths of fish by river were 541 mm in the Colorado, 519 mm in the Green, 498 mm in the White, and 577 mm in the Yampa (Figure 2). Few immature fish ($\leq$ 428 mm TL) were tagged on any river. All tagged fish from the Yampa River were over 350 mm TL, most were over 450 mm TL.

The virtual absence of fish less than 450 mm TL in the Yampa River suggests possible longitudinal separation of different life stages. Appearance of fish in the Yampa River after they reach 450 to 500 mm TL suggests that they recruit into this river after reaching sexual maturity (> 428 mm TL), possibly after migrating to the spawning area on the lower Yampa River. Tyus (1990) noted a net downstream movement of smaller fish and recruitment to adult stocks by upstream movement of larger fish. Samples from the Colorado

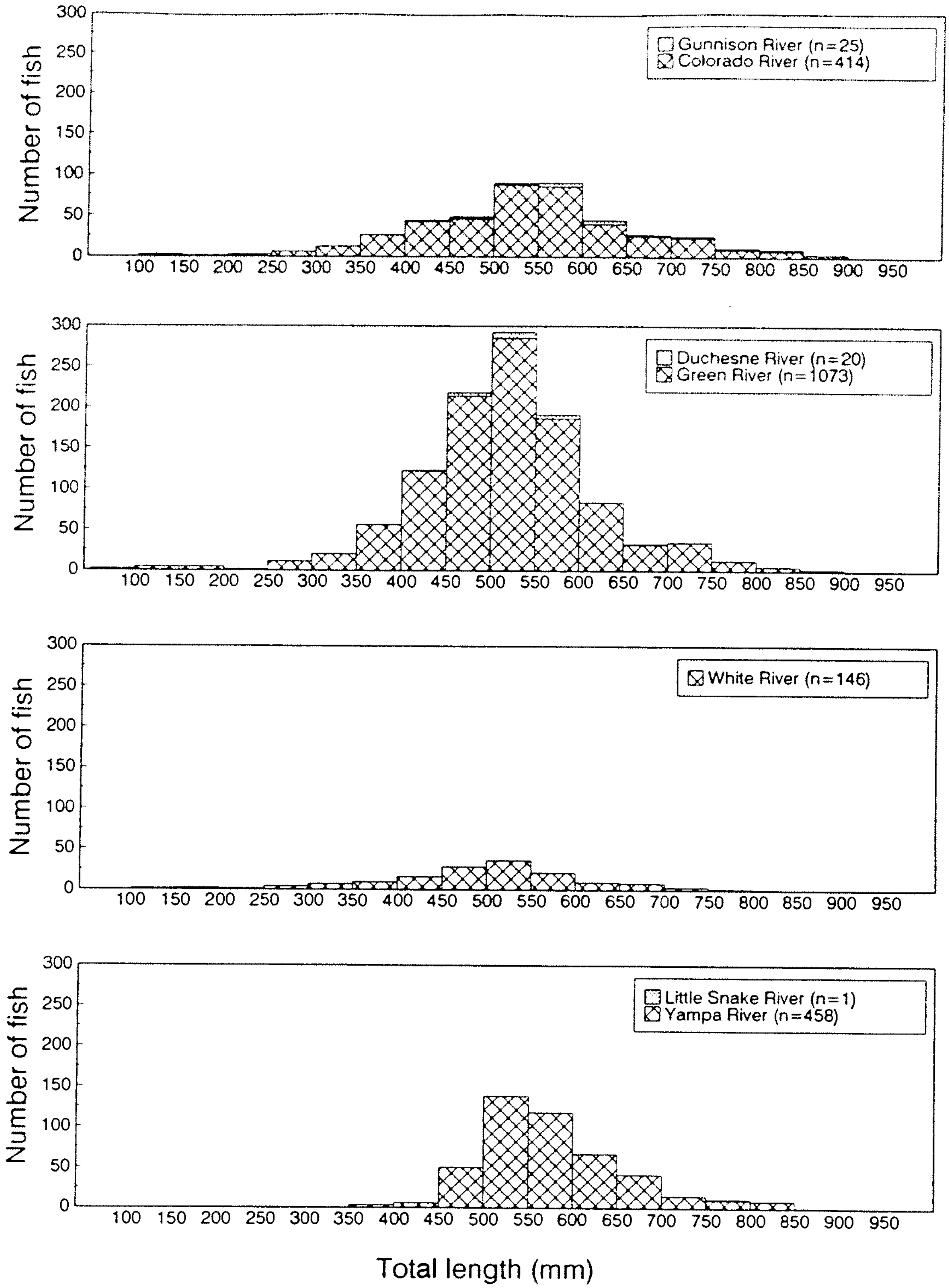

Figure 2. **Length frequency of tagged Colorado squawfish from the Upper Colorado River Basin, 1978-1989.**

and Green rivers included both large and small fish, but segregation of large and small fish may have occurred historically before impoundments blocked adult redistribution into upstream reaches.

Yearly length frequency was examined for Colorado squawfish collected from the Colorado, Green, and Yampa rivers during 1979-1988 and from the White River during 1981-1985. Other years were not included because the number of fish tagged during those years was small (n<10; Table 1). Yearly length-frequency distributions for fish from each river (Figures 3-9) were similar to their cumulative length-frequency distribution for the period 1978-1989 (Figure 2). Length-frequency distributions were consistent through the 10-year period. Fish between 500-600 mm TL were the most common sizes collected each year, suggesting continuous yearly recruitment into the sampled adult population. The consistent length-frequency distributions for each river suggested that gear was selecting fish within the 500-600 mm TL size range. The lack of 200-400 mm TL fish was probably a combination of gear selectivity and ineffective sampling of habitats or river reaches that contain fish in this size range.

Weight-length relationship

Least-squares regressions of weight-length relationships were calculated for each monthly sample with 10 or more mature (>428 mm TL) fish (Table 2).

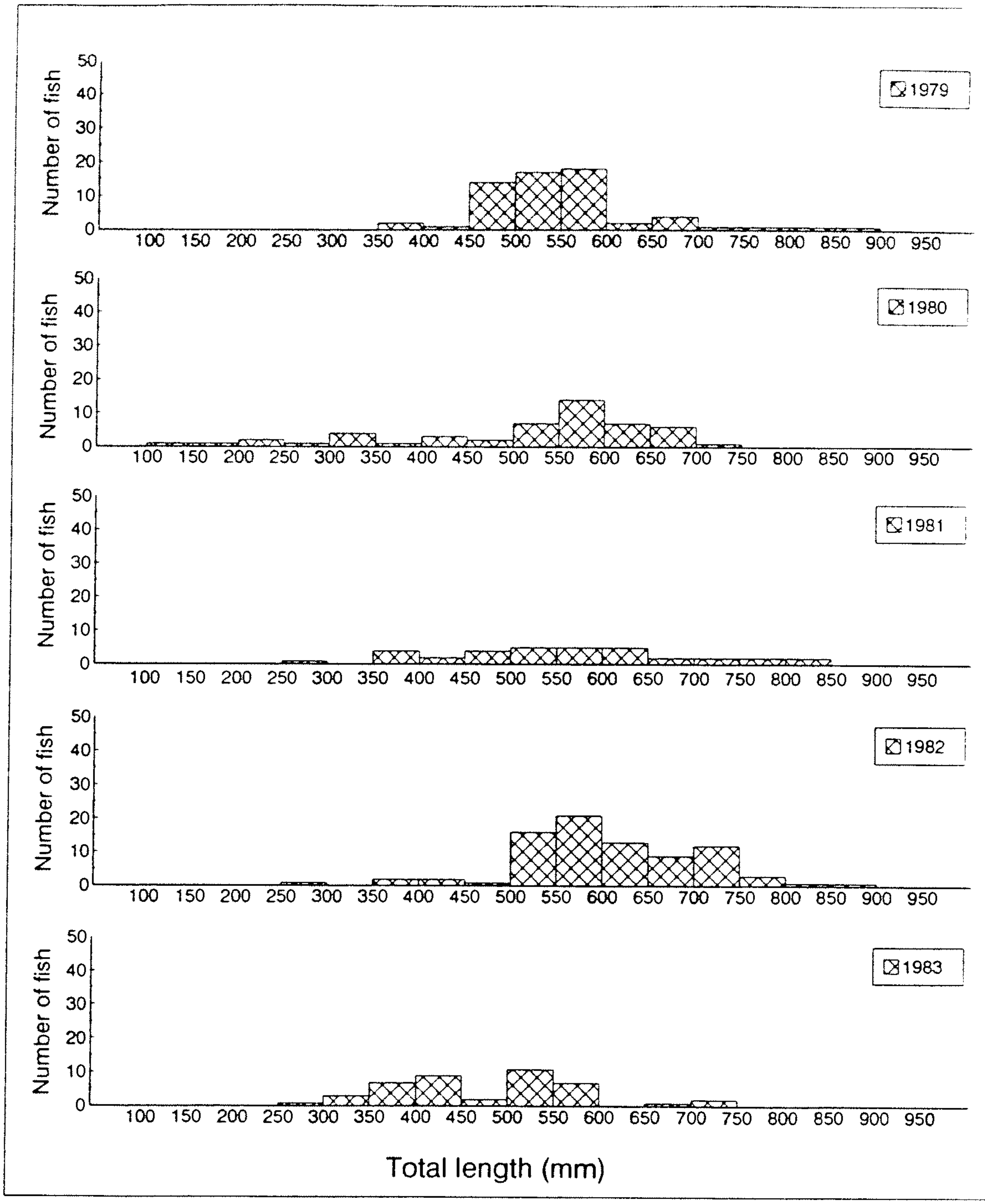

Figure 3. Yearly length frequency of tagged Colorado squawfish from the Colorado River, 1979-1983.

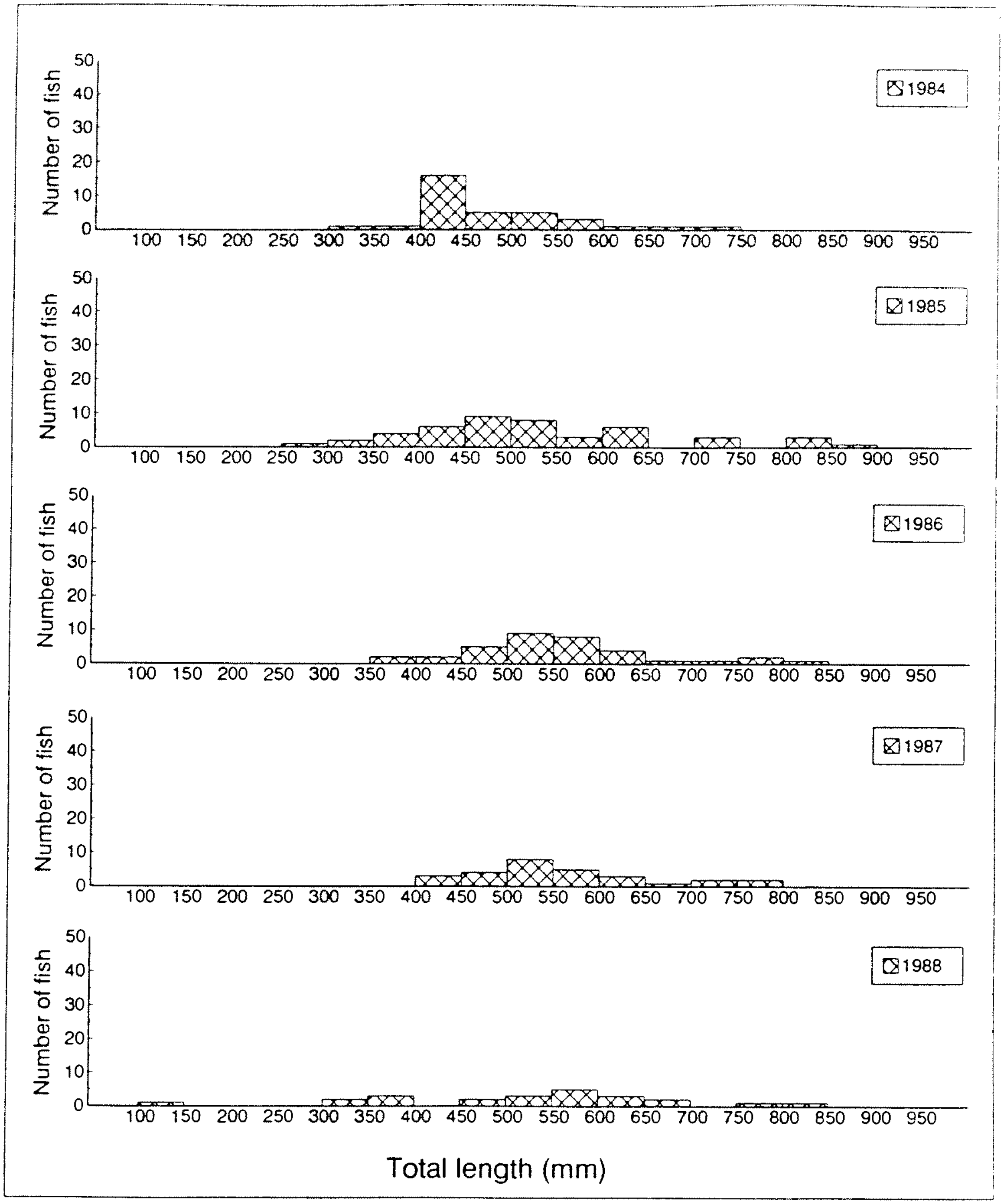

Figure 4. Yearly length frequency of tagged Colorado squawfish from the Colorado River, 1984-1988.

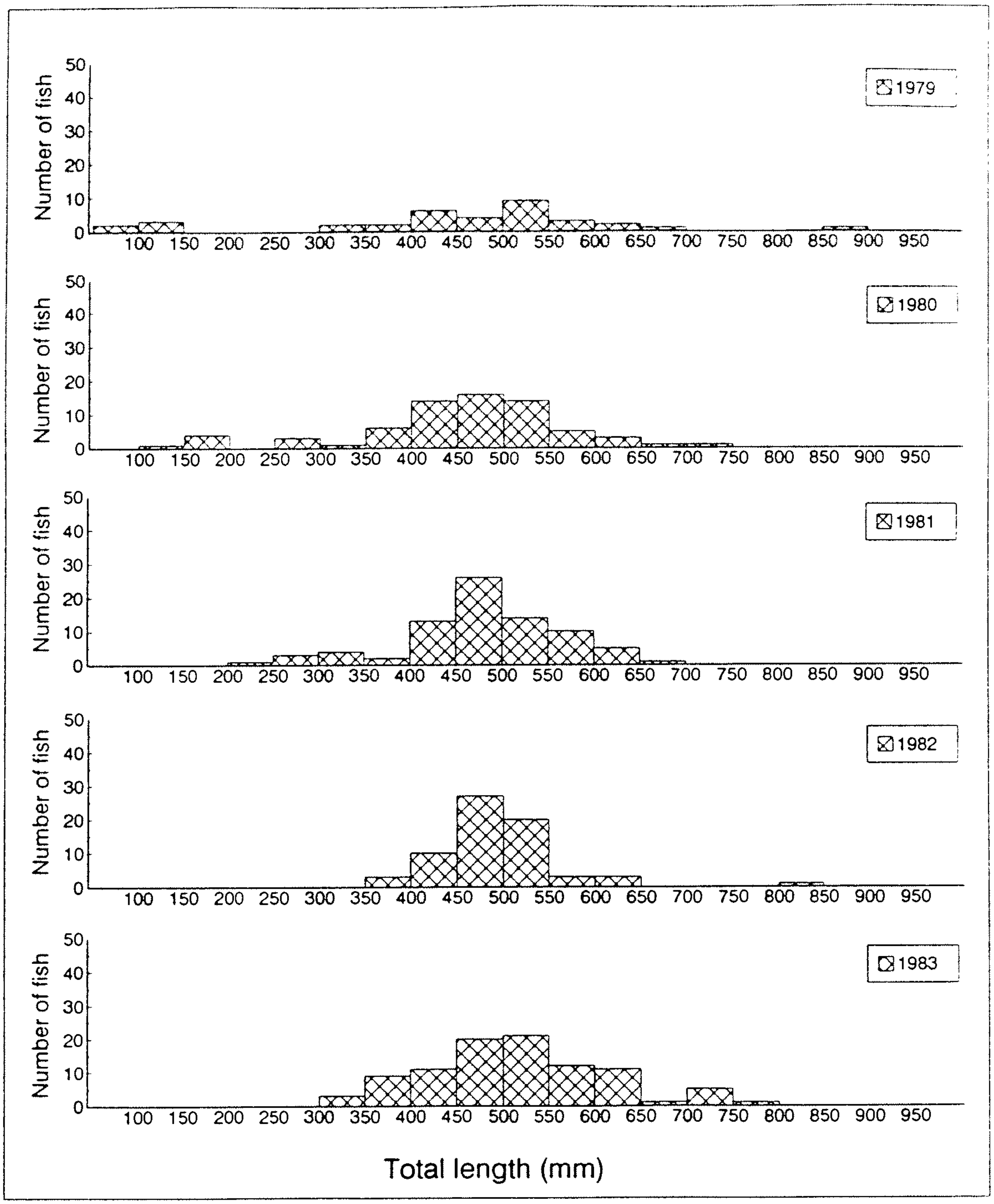

Figure 5. Yearly length frequency of tagged Colorado squawfish from the Green River, 1979-1983.

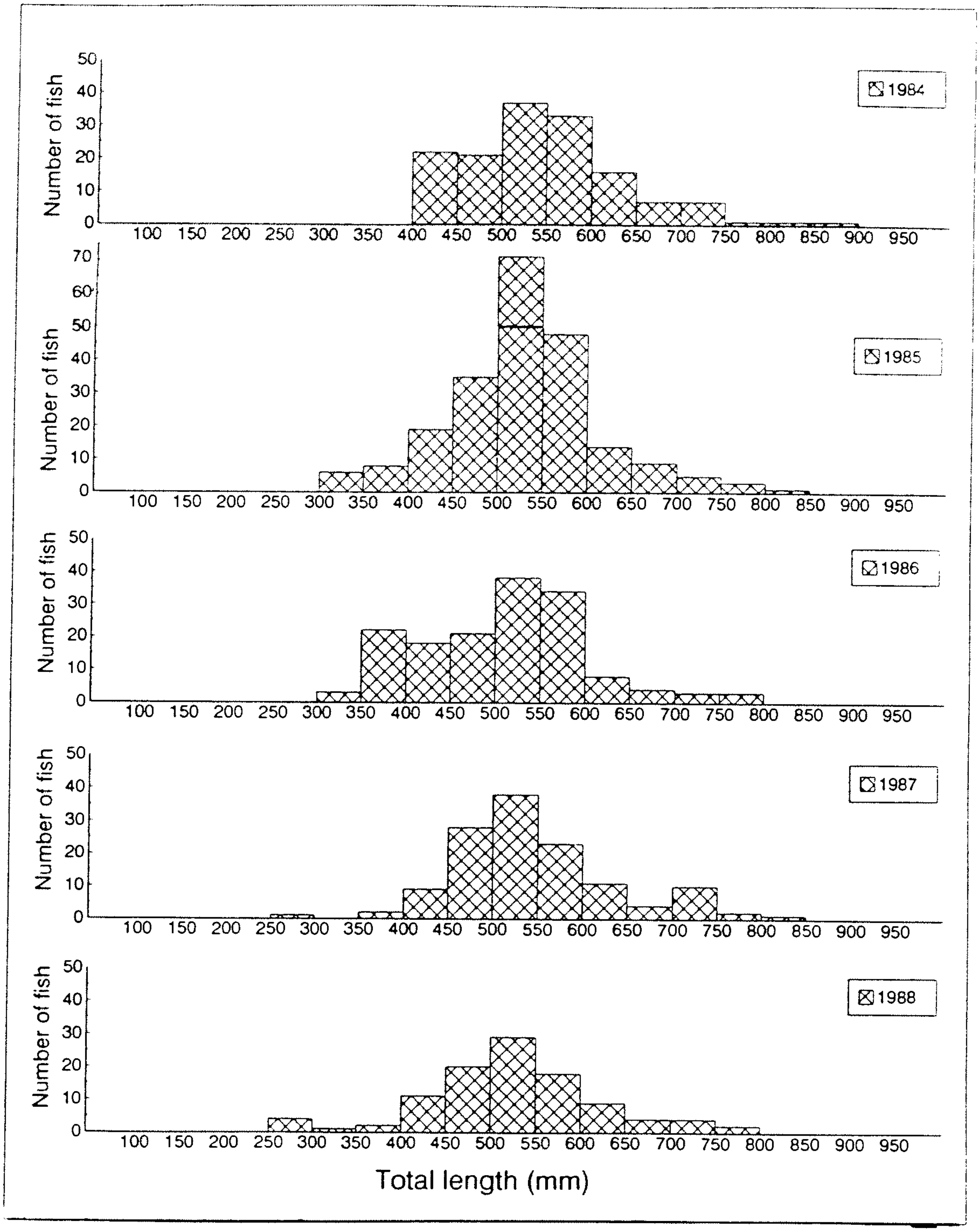

Figure 6. Yearly length frequency of tagged Colorado squawfish from the Green River, 1984-1988.

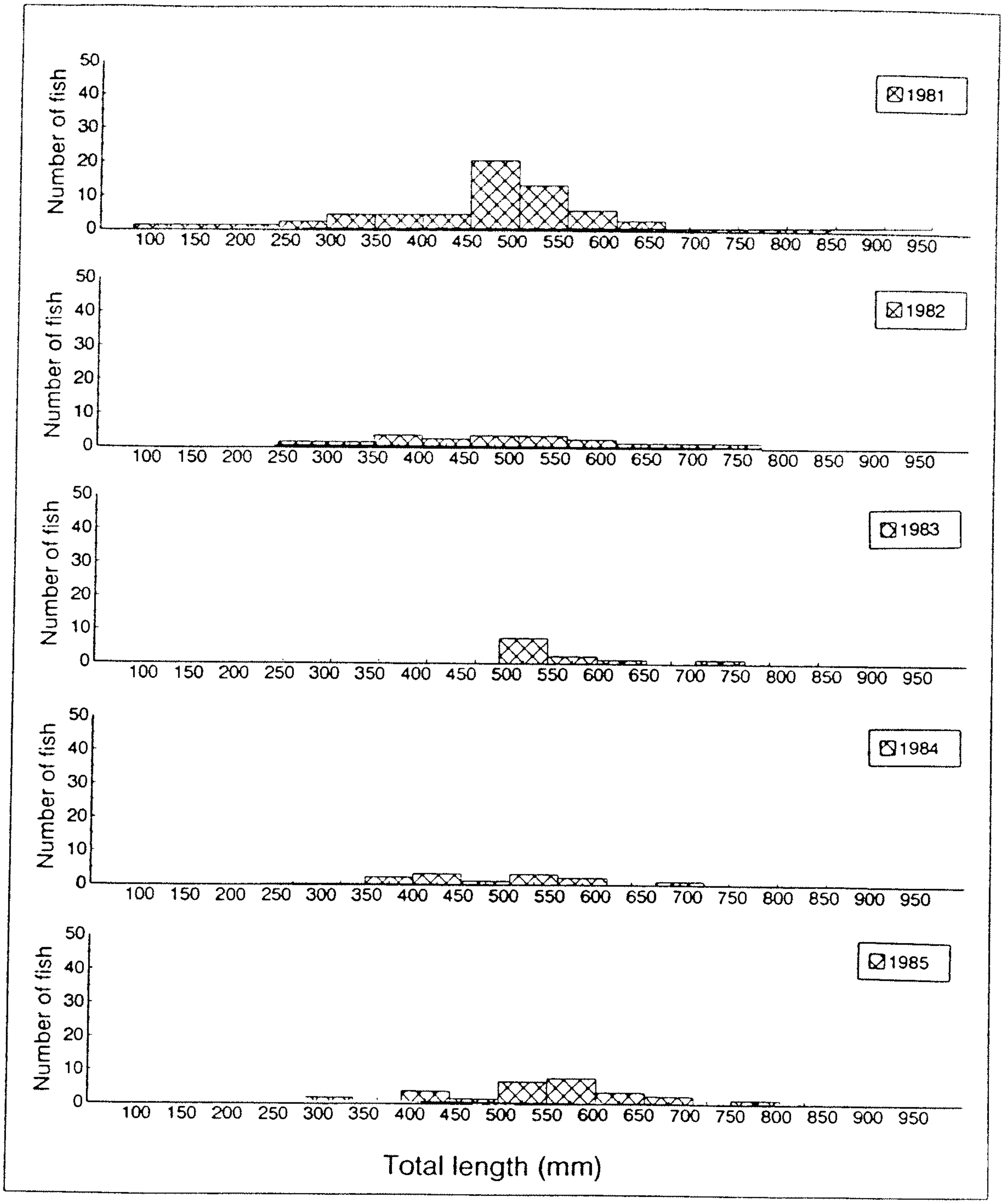

Figure 7. Yearly length frequency of tagged Colorado squawfish from the White River, 1981-1985.

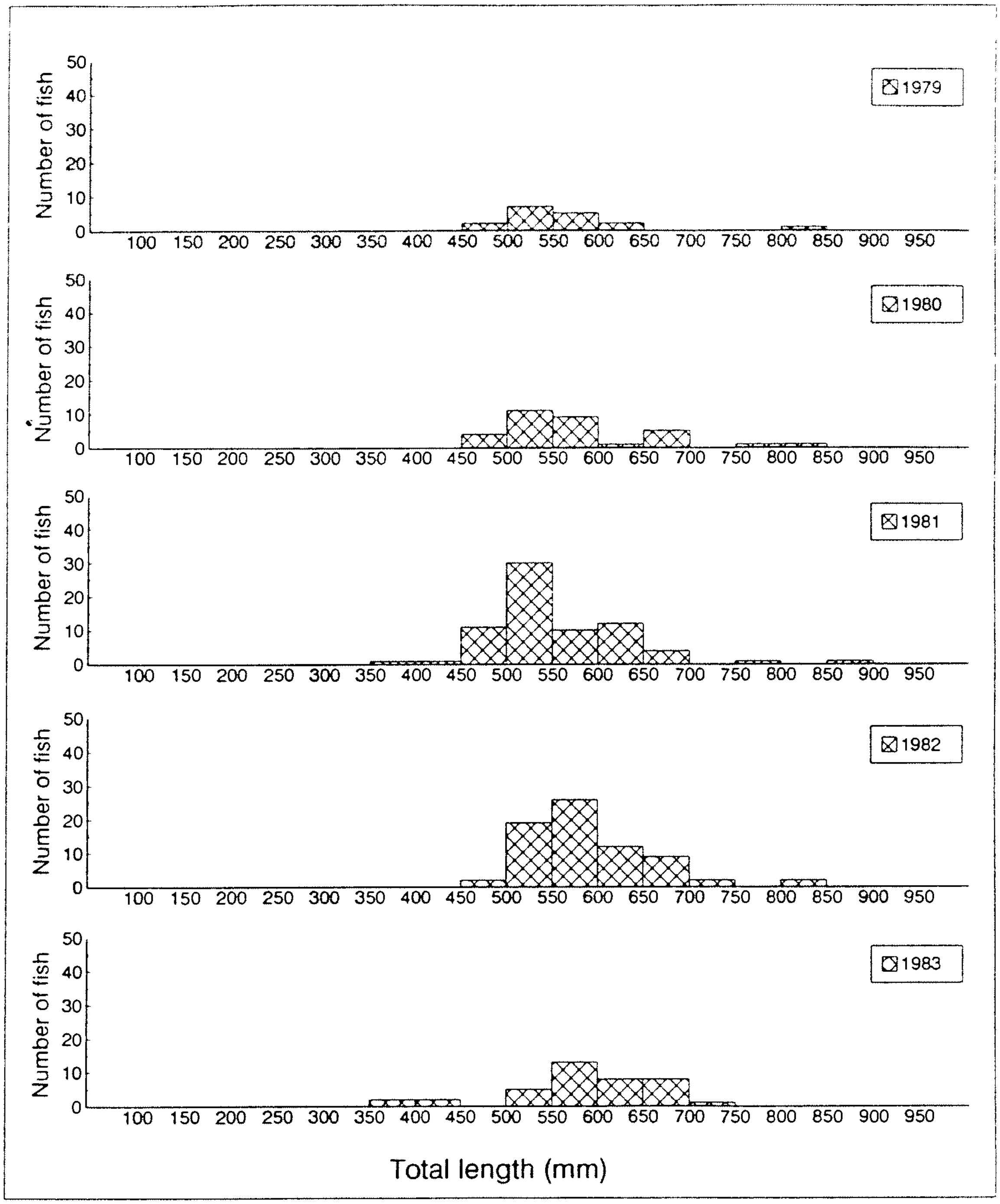

Figure 8. Yearly length frequency of tagged Colorado squawfish from the Yampa River, 1979-1983.

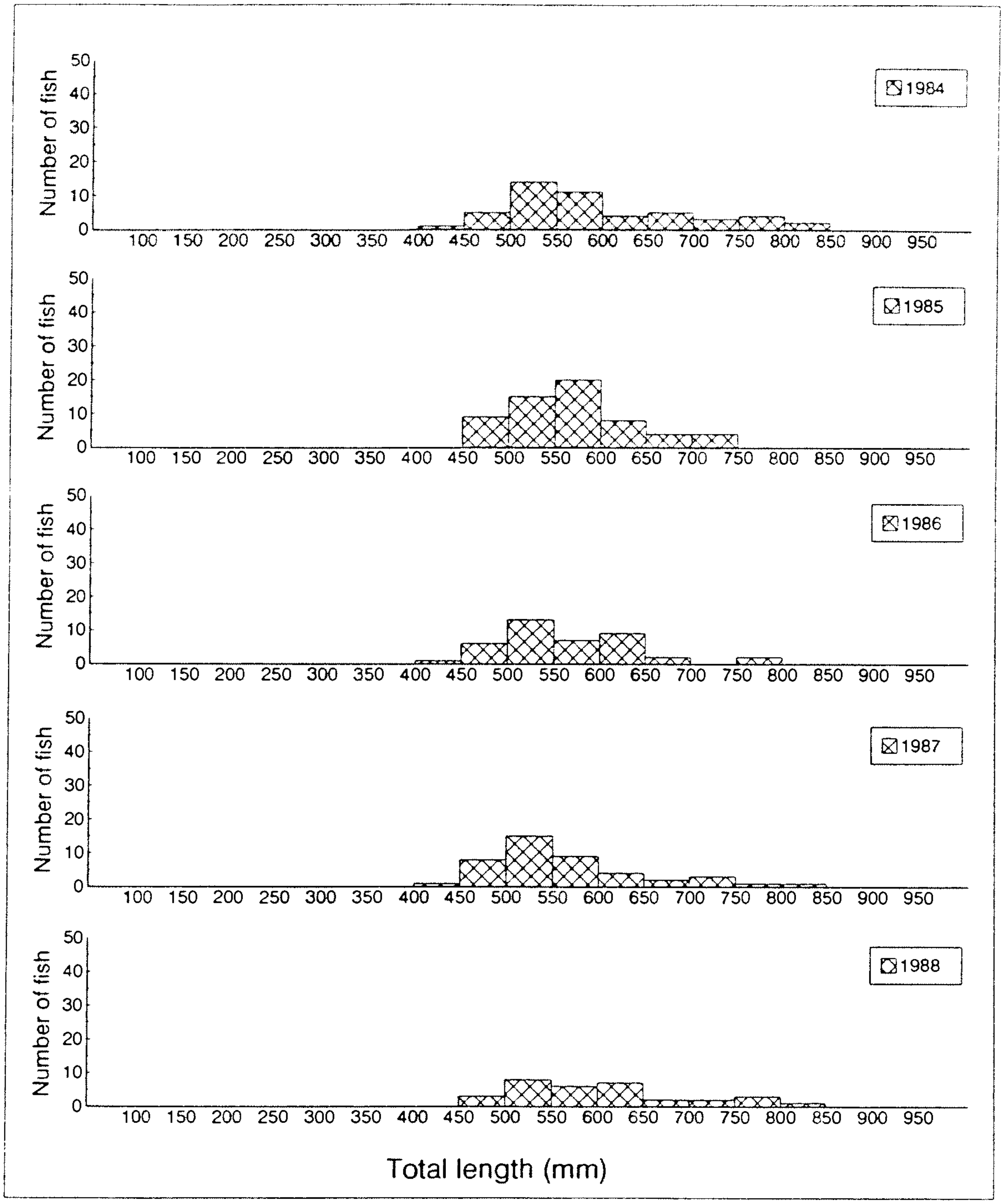

Figure 9. Yearly length frequency of tagged Colorado squawfish from the Yampa River, 1984-1988.

Table 2. Weight-length regression coefficients of mature (> 428 mm TL) Colorado squawfish from the Upper Colorado River Basin, 1978-1989. Coefficients were calculated from:
$\text{Log}_{10} W = \text{Log}_{10} a + b \text{Log}_{10} L$, where W is weight (g), L is total length (mm), $\text{Log}_{10} a$ equals y-intercept, and b equals slope.
n = number of fish.

	Colorado River slope = 3.463		**Green River** slope = 3.206	
	n	y-intercept	n	y-intercept
March	7	--	3	--
April	63	-6.418	153	-5.702
May	106	-6.356	459	-5.673
June	58	-6.334	44	-5.665
July	20	-6.402	142	-5.694
August	26	-6.360	52	-5.687
September	20	-6.402	27	-5.720
October	37	-6.385	44	-5.700
November	20	-6.414	1	--
Pooled among months		-6.384		-5.692

	White River slope = 3.156		**Yampa River** slope = 3.339	
	n	y-intercept	n	y-intercept
March	0	--	2	--
April	6	--	34	-6.023
May	25	-5.555	86	-6.014
June	14	-5.550	41	-6.007
July	11	-5.546	107	-6.032
August	32	-5.569	75	-6.048
September	9	--	18	-6.038
October	7	--	53	-6.018
November	3	--	3	--
Pooled among months		-5.555		-6.026

An analysis of co-variance indicated slopes of weight-length regressions between months within each river were not significantly different (Colorado River, $P = 0.3487$; Green River, $P = 0.6243$; White River, $P = 0.1225$; and Yampa River, $P = 0.8028$). The same slope was reported for each river, regardless of month. Intercepts were significantly different ($P < 0.05$) between months and were reported separately (Table 2). More fish were collected in some months than in others. To prevent these large samples from unduly influencing the weight-length relationship, intercepts from each month were given equal weight. Pooled weight-length regression equations by river were:

Colorado River	$\mathrm{Log}_{10}\, W = -6.384 + 3.463 * \mathrm{Log}_{10}\, L$,
Green River	$\mathrm{Log}_{10}\, W = -5.692 + 3.206 * \mathrm{Log}_{10}\, L$,
White River	$\mathrm{Log}_{10}\, W = -5.555 + 3.156 * \mathrm{Log}_{10}\, L$, and
Yampa River	$\mathrm{Log}_{10}\, W = -6.026 + 3.339 * \mathrm{Log}_{10}\, L$,

where W is weight (g), and L is total length (mm). Weight-length relationships for fish from the Colorado and Yampa rivers were very similar, as were relationships for fish from the White and Green rivers. Colorado squawfish collected from the Colorado or Yampa rivers were heavier at a given length than fish collected from the Green or White rivers (Figure 10).

Vanicek and Kramer (1969) reported the weight-length relationship for Colorado squawfish from the Green River as:

$$\mathrm{Log}_{10}\, W = -5.418 + 3.126 * \mathrm{Log}_{10}\, L.$$

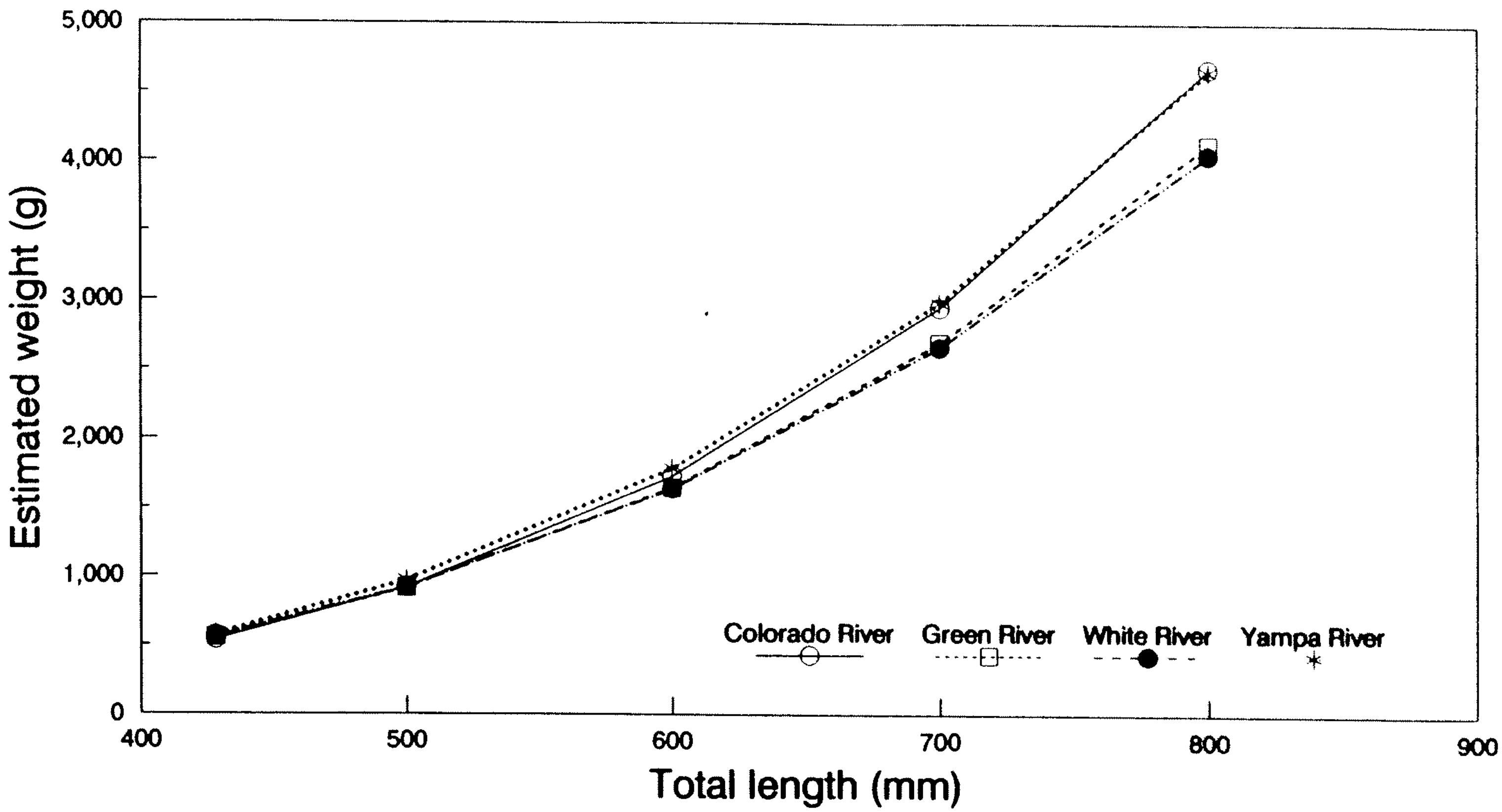

Figure 10. Estimated weights of Colorado squawfish from pooled weight-length relationships.

Seethaler (1978) reported weight-length relationships for Colorado squawfish from the Colorado, Green, and Yampa rivers as:

Green and Yampa rivers $\text{Log}_{10} W = -5.54 + 3.16 * \text{Log}_{10} L$,

Colorado River $\text{Log}_{10} W = -5.38 + 3.12 * \text{Log}_{10} L$, and

Green, Colorado, and Yampa combined

$$\text{Log}_{10} W = -5.38 + 3.11 * \text{Log}_{10} L.$$

Seethaler (1978) suggested that weight-length relationships for Colorado squawfish from the Green and Colorado rivers were not significantly different, supporting his hypothesis of a single genetic population. Although Vanicek and Kramer (1969) reported collecting 1469 Colorado squawfish from May 1964 to October 1966, they did not report the number of fish used in their regression analysis or when they were collected. Seethaler (1978) suggested that Vanicek and Kramer (1969) based the relationship on the 182 fish used in their scale analysis of age. Comparisons were not made with the previous weight-length regressions because my regression equations were based only on mature fish.

Pooled weight-length regressions reported here can be used to compare a fish to the average or expected weight of fish from the same river. The result would be useful in assessing the "health" of a captured fish and could influence field decisions, such as whether to implant a radio-transmitter in a fish. Relative condition of fish collected from different habitats might also be compared to determine if some habitats provide more optimum conditions for fish growth.

Fish condition

Mean *Kn* values were calculated monthly for mature (>428 mm TL) Colorado squawfish from each river (Figure 11). Except in the White River, condition generally increased in the spring to a maximum in June. Fish from the White River did not have dramatic gains and losses as fish from the other rivers. Maximum condition of fish in June was probably due to an increase in fatty reserves or gametes in preparation for spawning. Post-spawning loss of condition occurred in July for fish from the Colorado and Green rivers and August for fish from the Yampa and White rivers. Weight loss was probably due to long migration or release of gametes. Fish from each river regained weight in late summer or early fall after the migratory period.

Age and growth

Scales were removed from 272 tagged Colorado squawfish collected between 1979 and 1989; 64 additional scale samples were collected from smaller untagged fish collected from the Green River in 1990. Regenerated scales comprised about 25% of each scale sample. False checks were distinguished from true annuli because they did not form a complete ring around the scale. Scales often showed erosion along the most posterior edge but seldom were eroded along the anterior or lateral margins. A few were eroded along one, but usually not both, of the lateral margins. When several scales were available from one fish, the scale whose shape was consistent with

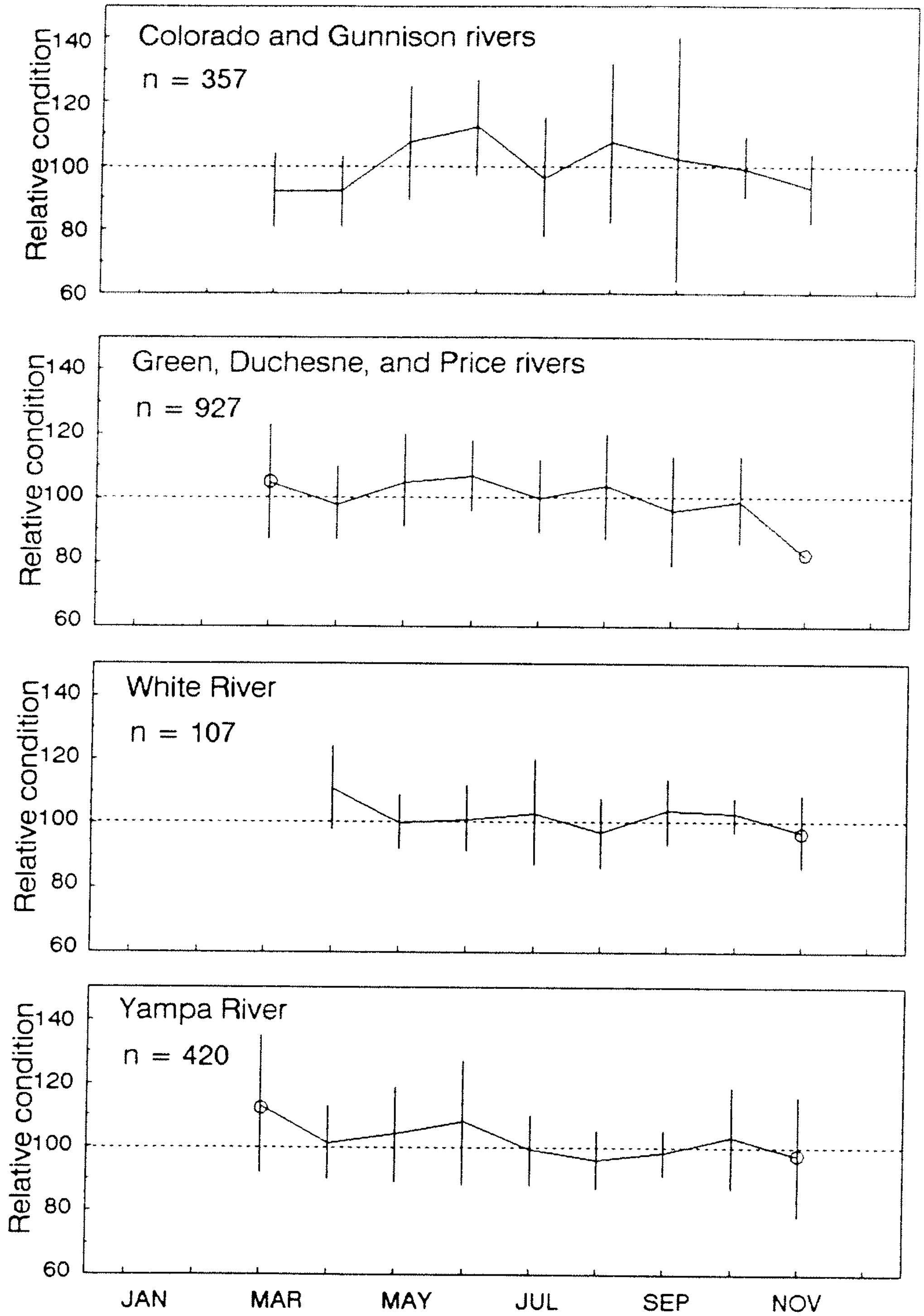

Figure 11. Seasonal variation of mean relative condition (*Kn*) of mature (> 428 mm TL) Colorado squawfish from the Upper Colorado River Basin, 1978-1989. Circles indicate mean from samples of less than five fish. Vertical bars are 95% confidence interval of the mean relative condition.

previous scale shapes was chosen for ageing. The first three or four annuli were often difficult to distinguish; older annuli were more discrete and obvious. The first annulus was identified as the boundary between slowly (close) and rapidly (spaced) deposited circuli. Other annuli were distinguished by a discrete dark band of closely spaced circuli or by patterns of cutting over. Cutting over occurs where outer circuli flare outward or end abruptly during slow growth and are surrounded by new circuli that form completely when rapid growth resumes (Jearld 1983).

A total of 336 scales was used to plot a fish-length to scale-radius relationship (Figure 12). It was described best by the linear equation:

$$L = 185.6358\ SR + 45.1507 \quad (r^2 = 91\%),$$

where L is fish total length (mm), and SR is scale radius. Standard error was 7.6754 for the intercept and 3.1849 for the slope. The estimated y-intercept (45 mm) was very close to the identified size (35-40 mm TL) of Colorado squawfish at scale formation (Vanicek and Kramer 1969). Of 336 fish used in the body-scale relationship, 10 were removed from further ageing analysis because of indistinct annuli. The remaining 326 fish were aged and used in back-calculating length at each annulus.

Apparently the first annulus was not observed during ageing. Seethaler (1978) and Musker (1981) also failed to detect and measure the first annulus. Although Vanicek (1969) reported measurements for the first annulus, it may not form on most Colorado squawfish. Lack of first-year annuli is apparently

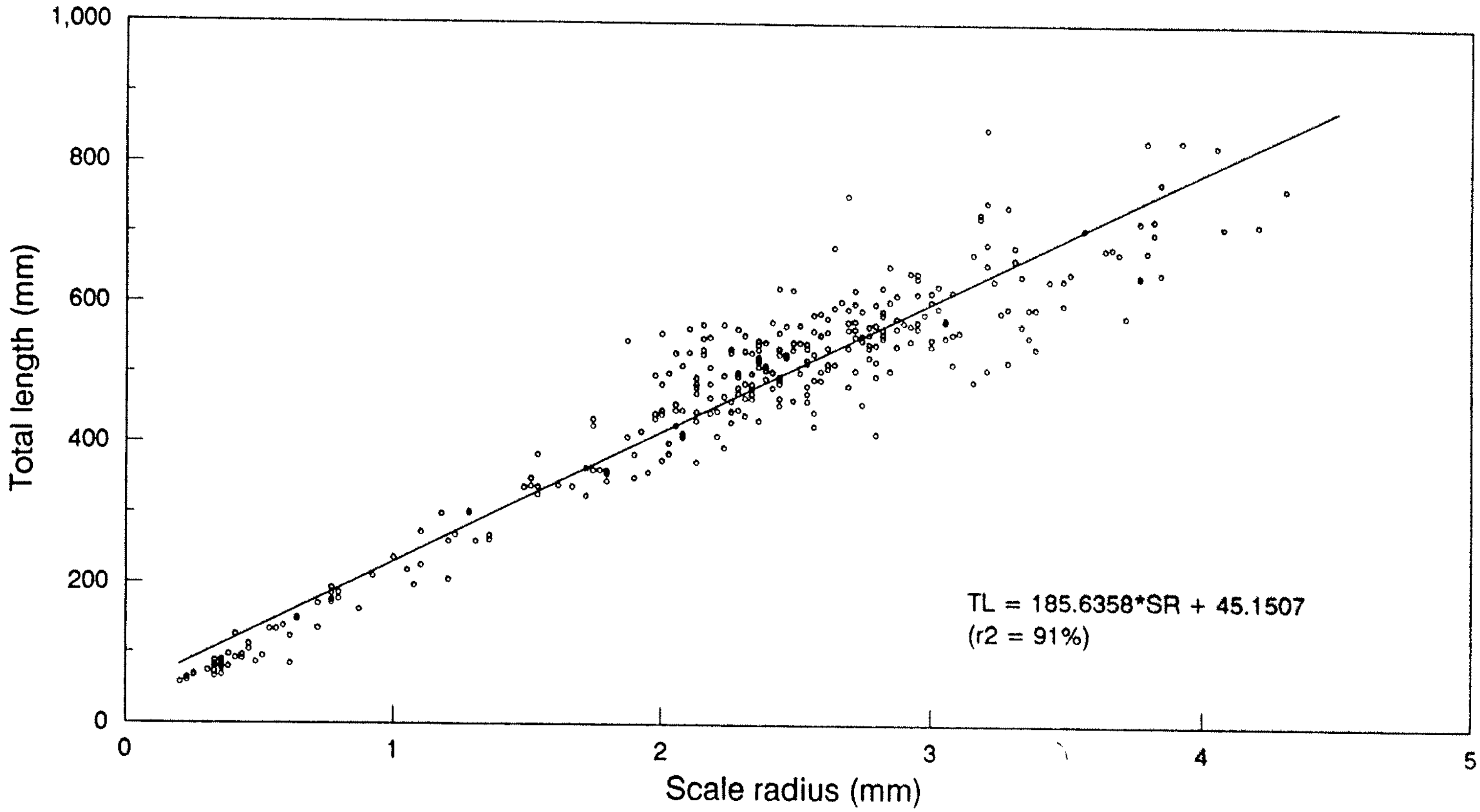

Figure 12. Fish-length to scale-radius relationship for 336 Colorado squawfish from the Upper Colorado River Basin, 1978-1990.

common in salmonids within the Intermountain West (Lentsch and Griffith 1987). If scale formation occurs at 35-40 mm TL, then Colorado squawfish might enter the winter period without scales. In the Green River between 1964 and 1966, age-0 fish averaged less than 25 mm TL in September (Vanicek and Kramer 1969). Valdez (1990) observed average lengths of 30.6, 34.0, and 38.0 mm for age-0 fish from 1986, 1987, and 1988 year classes, respectively, collected in October from Cataract Canyon. Age-0 Colorado squawfish collected in October 1979-1985 and 1987-1988 from the upper and lower Green River averaged 40 mm TL and ranged 29-47 mm TL (Tyus and Haines 1991). If fish were large enough to have scales going into the winter, the annulus would probably not be discernible from the scale focus.

I estimated annulus formation occurred in late May based on observations of annuli on the margin of scales taken from fish in late May and early June. Vanicek and Kramer (1969) identified annulus formation in early June. Time of annulus formation is significant because it identifies when growth resumes after the winter period. Resumption of growth is caused by a combination of increased food and temperature and probably varies with habitat. If a fish can exploit a warmer habitat, such as a shallow backwater in early spring, it is likely to start growing sooner than a fish using the colder main channel.

Age validation

Beamish and McFarlane (1983) identified that only mark-recapture and known-age fish can validate all age classes in a population. Estimated ages from scales were validated up to age 10 with scales from two known-age, hatchery-reared Colorado squawfish. These fish were hatched in June 1974, at Willow Beach National Fish Hatchery, Arizona, and transferred to Dexter National Fish Hatchery, New Mexico, until they were stocked in the Green River near Green River, Utah, in April 1980 at 6 years of age. Two of these fish were recaptured and killed in May 1984. They were 415 and 460 mm TL at capture in 1984 and were 10 years old at death. The two scale samples were aged without knowledge of their origin or age, and they contained nine annuli. Adding the missing first annulus resulted in a correct age of 10 years old. Back-calculated lengths at stocking (233 and 322 mm TL) were similar to reported lengths (200-300 mm TL) for fish stocked in 1980 (C. McAda, USFWS, Grand Junction, Colorado, personal communication), validating back-calculated lengths.

Additional validation was attempted with tag-recapture data but was less successful. Readable scales were taken at both capture and recapture from only 18 of 278 recaptured Colorado squawfish. Time interval between capture and recapture ranged from less than 1 year to 6 years. Known time interval was compared to estimated difference between capture and recapture. Estimated ages of these fish ranged from 7 to 13 years at first capture.

Recapture interval was correctly predicted for seven of the 18 fish. Recapture intervals for 11 fish were incorrectly determined. Ten of these were incorrect by plus or minus 2 years of the known time interval. A possible reason for differences between the expected and observed time interval could be incorrect identification of the last annulus. Annuli were very closely spaced at the edges of scales from older fish. It was difficult to identify the last annulus on older fish collected between May and June. Incorrectly ageing a scale by only 1 year at both capture and recapture could account for a total difference of up to 2 years. The recapture interval for one fish, estimated 15 years old at first capture, was underestimated by 6 years, demonstrating that errors may increase with older fish.

Underestimation of age has been shown for many fishes that were aged without proper validation (Beamish and McFarlane 1983, 1987). Usually these ages were estimated from scales. Other bony structures such as otoliths have proven successful for ageing older fishes, but even these determinations need validation. Older ages do not necessarily mean more accurate ages. The cui-ui *Chasmistes cujus*, a catostomid endemic to Pyramid Lake, Nevada, was thought to be short lived until opercula were aged up to 41 years (Scoppettone 1988). Ages were validated by following several known year classes. The longevity of razorback sucker *Xyrauchen texanus*, another large catostomid, was extended to 44 years based on ageing with otoliths (McCarthy and Minckley 1987). Scoppettone (1988) aged three Colorado squawfish and obtained a maximum age of 26 years. Opercula were used to estimate ages, but these ages were not validated.

Ages greater than maximum validated age must not be considered accurate (Beamish and McFarlane 1983). Colorado squawfish ages were validated up to age 10, age and growth data above this age are suspect and should not be used in additional population parameter estimates until proven accurate. Incorrectly ageing older fish can result in an accumulation of ages at the age where the method fails (Beamish and McFarlane 1987). There was an accumulation of Colorado squawfish between 8 and 10 years old in my study, but this may reflect the large number of collected fish that were 500 to 600 mm TL (Figures 3-9), the expected length of fish in this age span.

Age composition

Age composition was determined for Colorado squawfish collected from the Colorado, Green, White, and Yampa rivers (Figure 13). Colorado River samples were small and inadequate with only 14 fish. Fish from the Green River were relatively younger than those from its primary tributary , the Yampa River. This was partially due to 60 untagged smaller fish collected in 1990 that were included in the Green River sample. The Yampa River still contained more older fish than any other river, suggesting that fish populate upper-reach tributaries after attaining sexual maturity. Radio-telemetry and tag-recapture information confirmed this. Smaller fish have been tagged in the lower Green

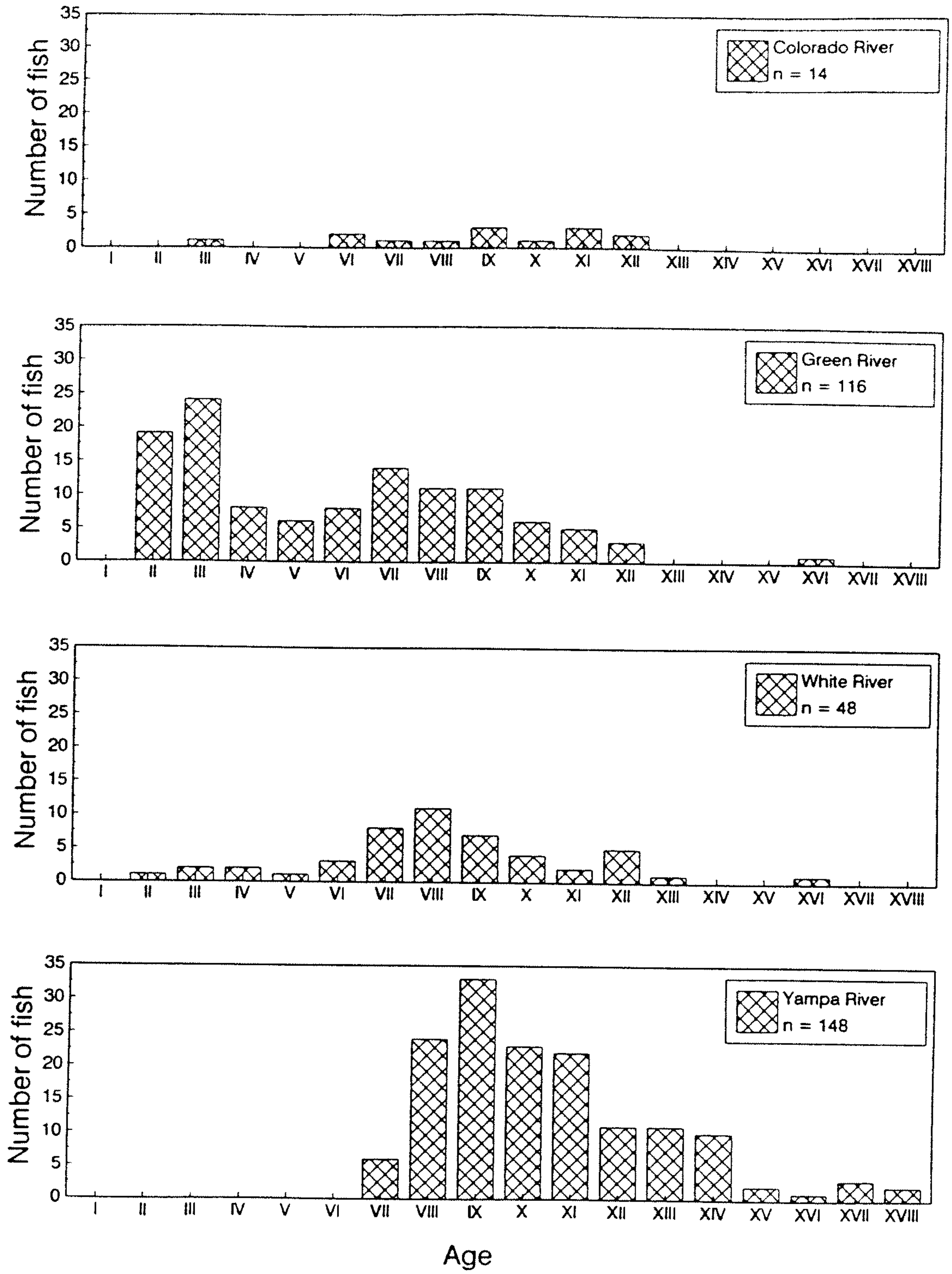

Figure 13. Age composition of Colorado squawfish from the Upper Colorado River Basin, 1978-1990. The Green River sample includes 64 small, untagged fish collected in 1990.

River and recaptured both at the Yampa River spawning area and at over-wintering sites in the upper Yampa River (Tyus 1990). Colorado squawfish also return to their over-winter sites each year after spawning (Wick and Hawkins 1989).

Back-calculation of length

Estimated length at each previous age from scales described the growth of each population. Back-calculated lengths of Colorado squawfish from the Colorado, Green, White, and Yampa rivers were treated separately and combined (Tables 3-7). Length at age 1 was unknown due to lack of a first annulus on any scale. The shortest fish length calculated from an annulus was 57 mm TL. Only 25 fish were under 75 mm TL when the first observable annulus was formed. Back-calculated length measured at first annulus should be similar to lengths of age-0 fish collected at the end of their first growing season or at the beginning of their second growing season.

Back-calculated length was plotted against age for each population of Colorado squawfish (Figure 14). Growth rates of fish younger than 7 years were similar among the four rivers. After age 7, fish reached sexual maturity, and growth rates varied between rivers. Greater variation past this age may be due to smaller sample sizes of older fish, differences between mature males and females, natural variation between different populations, or compounding of the large variation in scale sizes of larger (older) fish (Figure 12).

Table 3. Back-calculated total lengths (TL) of 326 Colorado squawfish from the Colorado, Green, White and Yampa rivers combined, 1978-1990. n = number of fish.

			Mean estimated total length (mm) at annulus																	
Age Group	n	Mean TL	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
I	0	-	-																	
II	20	84	-	75																
III	27	128	-	84	118															
IV	10	230	-	90	151	208														
V	7	302	-	94	155	221	282													
VI	13	369	-	98	155	205	274	331												
VII	29	462	-	98	164	240	317	381	429											
VIII	47	496	-	101	157	227	300	365	413	466										
IX	54	521	-	98	155	220	289	349	401	449	492									
X	34	533	-	99	152	222	284	339	388	431	473	511								
XI	32	582	-	97	150	215	277	332	379	429	478	523	562							
XII	21	614	-	90	143	212	272	329	382	430	477	523	565	597						
XIII	12	635	-	95	147	203	264	316	371	415	471	517	558	591	624					
XIV	10	653	-	94	150	206	268	322	379	426	466	500	535	574	613	644				
XV	2	719	-	85	126	248	294	339	381	458	502	542	569	614	650	675	698			
XVI	3	678	-	87	143	193	230	280	331	370	406	447	475	513	544	576	609	663		
XVII	3	792	-	98	150	212	264	314	359	407	455	501	549	587	634	669	702	740	776	
XVIII	2	804	-	84	140	173	242	299	340	373	436	474	512	570	621	649	679	717	748	776
Mean			-	94	150	220	286	345	396	440	478	514	554	586	615	641	669	705	764	776
95 % CI			-	2	3	5	5	6	6	7	8	10	14	19	25	33	43	44	51	60
n			0	326	306	279	269	262	249	220	173	119	85	53	32	20	10	8	5	2

Table 4. Back-calculated total lengths (TL) of 14 Colorado squawfish from the Colorado River, 1978-1990. n= number of fish.

			Mean estimated total length (mm) at annulus											
Age Group	n	Mean TL	1	2	3	4	5	6	7	8	9	10	11	12
I	0	-	-											
II	0	-	-	-										
III	1	77	-	66	77									
IV	0	-	-	-	-	-								
V	0	-	-	-	-	-	-							
VI	2	415	-	95	167	198	295	340						
VII	1	465	-	90	159	213	297	356	396					
VIII	1	502	-	99	147	235	283	385	449	483				
IX	3	557	-	99	148	205	272	334	404	456	509			
X	1	595	-	115	148	250	329	385	446	488	525	595		
XI	3	597	-	93	142	190	243	294	339	403	472	519	558	
XII	2	666	-	84	132	228	273	364	421	483	562	600	631	657
Mean			-	93	143	210	276	340	397	451	510	559	587	657
95 % CI			-	7	14	15	22	23	30	34	45	74	84	141
n			0	14	14	13	13	13	11	10	9	6	5	2

Table 5. Back-calculated total lengths (TL) of 116 Colorado squawfish from the Green River, 1978-1990. n = number of fish.

Age Group	n	Mean TL	Mean estimated total length (mm) at annulus 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
I	0	-	-															
II	19	80	-	74														
III	24	121	-	84	118													
IV	8	214	-	89	150	205												
V	6	292	-	95	154	224	281											
VI	8	354	-	96	152	206	271	327										
VII	14	411	-	97	162	227	299	355	402									
VIII	11	456	-	99	143	209	274	335	387	436								
IX	11	456	-	95	147	204	267	322	371	410	447							
X	6	508	-	101	157	221	281	323	374	422	462	503						
XI	5	522	-	98	137	193	263	319	359	404	448	485	519					
XII	3	611	-	87	152	230	308	366	405	439	485	529	566	597				
XIII	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
XIV	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
XV	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XVI	1	718	-	77	137	196	219	301	384	425	457	480	517	553	594	636	663	718
Mean			-	90	143	213	279	335	384	422	456	500	534	586	594	636	663	718
95 % CI			-	3	7	8	11	13	14	16	20	30	45	93	0	0	0	0
n			0	116	97	73	65	59	51	37	26	15	9	4	1	1	1	1

Table 6. Back-calculated total lengths (TL) of 48 Colorado squawfish from the White River, 1978-1990. n = number of fish.

			Mean estimated total length (mm) at annulus															
Age Group	n	Mean TL	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
I	0	-	-															
II	1	172	-	96														
III	2	235	-	93	143													
IV	2	294	-	93	152	223												
V	1	360	-	86	158	203	284											
VI	3	378	-	105	153	210	270	336										
VII	8	483	-	98	152	231	310	374	421									
VIII	11	493	-	101	162	218	286	356	402	451								
IX	7	520	-	100	155	214	277	343	396	446	490							
X	4	536	-	103	148	212	262	322	371	410	467	507						
XI	2	552	-	104	184	233	268	323	358	409	447	482	520					
XII	5	588	-	94	145	198	247	294	348	402	446	494	535	567				
XIII	1	561	-	92	139	182	233	280	331	361	425	450	493	510	540			
XIV	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
XV	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
XVI	1	676	-	92	165	224	275	309	335	356	378	416	437	467	501	535	574	629
Mean			-	99	155	216	279	340	389	428	461	487	516	544	520	535	574	629
95 % CI			-	3	8	11	14	16	17	19	23	27	36	48	0	0	0	0
n			0	48	47	45	43	42	39	31	20	13	9	7	2	1	1	1

Table 7. Back-calculated total lengths (TL) of 148 Colorado squawfish from the Yampa River, 1978-1990. n = number of fish.

Age Group	n	Mean TL	Mean estimated total length (mm) at annulus 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
I	0	-	-																	
II	0	-	-	-																
III	0	-	-	-	-															
IV	0	-	-	-	-	-														
V	0	-	-	-	-	-	-													
VI	0	-	-	-	-	-	-	-												
VII	6	555	-	100	188	288	374	454	509											
VIII	24	515	-	102	162	238	319	381	430	485										
IX	33	539	-	98	158	229	300	361	411	461	506									
X	23	537	-	97	152	223	287	344	392	434	474	511								
XI	22	597	-	97	152	222	286	341	391	440	489	536	576							
XII	11	617	-	90	142	211	273	328	384	431	474	520	566	601						
XIII	11	642	-	96	148	205	266	319	374	420	475	523	564	599	631					
XIV	10	653	-	94	150	206	268	322	379	426	466	500	535	574	613	644				
XV	2	719	-	85	126	248	294	339	381	458	502	542	569	614	650	675	698			
XVI	1	641	-	91	128	160	196	228	274	329	384	444	471	517	536	559	591	641		
XVII	3	792	-	98	150	212	264	314	359	407	455	501	549	587	634	669	702	740	776	
XVIII	2	804	-	84	140	173	242	299	340	373	436	474	512	570	621	649	679	717	748	776
Mean			-	97	154	225	293	351	402	446	484	518	560	590	623	648	681	716	764	776
95 % CI			-	2	4	7	7	8	8	9	9	11	15	21	25	35	47	53	51	60
n			0	148	148	148	148	148	148	142	118	85	62	40	29	18	8	6	5	2

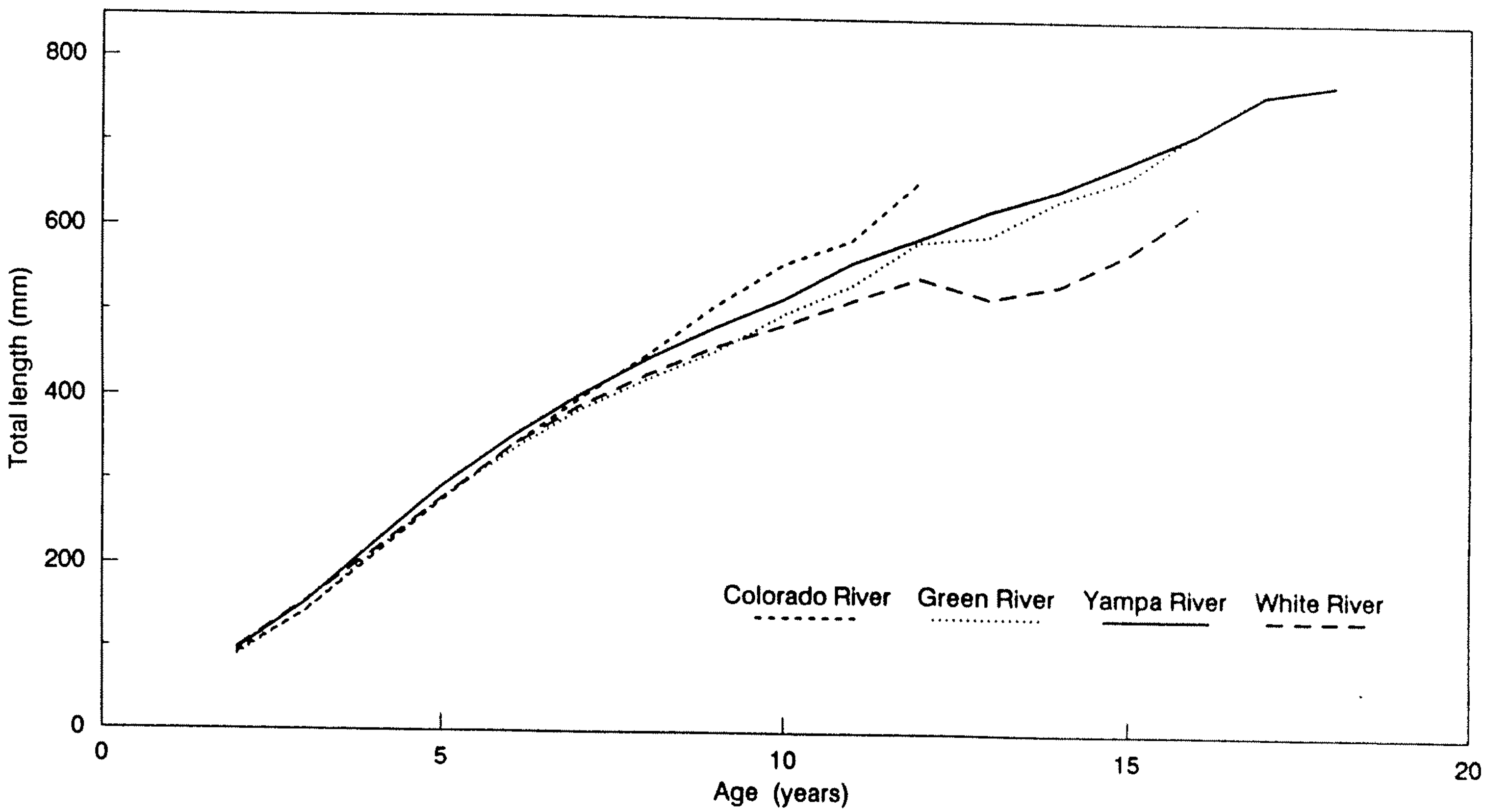

Figure 14. Average back-calculated lengths of Colorado squawfish from the Upper Colorado River Basin, 1978-1990.

Musker (1981) used several small samples to estimate the y-intercept (*a*) value from equation (6). These intercept values were not accurate representations of the body-length to scale-radius relationship and caused inaccurate back-calculation of lengths at each annulus. Carlander (1981) warned of calculating *a* from inadequate samples and suggested using a standard *a* for each species. Using the *a* (45.151) I calculated from 336 Colorado squawfish (Figure 6), lengths at each annulus were recalculated with equation (7) from annuli measurements reported by Musker (Appendix Table A-1). These adjusted calculations were used in further comparisons.

Back-calculated lengths in my study were shorter than lengths at age reported by other authors (Table 8). Fish tended to be 1 year older for a given size when compared with lengths at age from previous studies (Figure 15). The oldest fish aged by Musker (1981) was an 879-mm-TL, 13-year-old Yampa River fish. An 11-year-old female, 610 mm long was the oldest fish aged by Vanicek and Kramer (1969). Seethaler's (1978) oldest fish was also 11 years old. The two oldest fish I aged were from the Yampa River and were 18 years old and over 800 mm long. Oldest fish from other rivers were 16 (Green and White rivers) and 12 years (Colorado River).

Table 8. Summary of back-calculated total lengths of Colorado squawfish from this and previous studies in the Upper Colorado River Basin. n = number of fish.

		Mean estimated total length (mm) at annulus																	
	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Vanicek and Kramer (1969), 1964-1966:																			
Green River	182	44	95	162	238	320	391	454	499	536	570	600							
Seethaler (1978), 1974-1976:																			
Colorado River	68	-	106	198	285	355	411	453	495	531	570	619							
Green River	63	-	71	172	269	342	400	449	486	518	552	600							
Colorado, Green, and Yampa rivers combined	131	-	90	186	278	350	406	451	491	524	557	604							
Musker (1981) original data, 1979-1981:																			
Colorado River	10	-	116	213	296	364	436	495	596	643									
Green River	103	-	150	211	285	346	413	454	511	548									
White River	9	-	399	421	448	474	498												
Yampa River	26	-	195	245	309	366	422	465	502	540	583	666	767	824					
Musker (1981) recalculated data, 1979-1981:																			
Colorado, Green, White, and Yampa rivers combined	139	-	123	194	275	349	407	461	500	546	586	629	680	848					
Hawkins, 1978-1990:																			
Green River	116	-	90	143	213	279	335	384	422	456	500	534	586	594	636	663	718		
Colorado River	14	-	93	143	210	276	340	397	451	510	559	587	657						
White River	48	-	99	155	216	279	340	389	428	461	487	516	544	520	535	574	629		
Yampa River	148	-	97	154	225	293	351	402	446	484	518	560	590	623	648	681	716	764	776
Colorado, Green, White, and Yampa rivers combined	326	-	94	150	220	286	345	396	440	478	514	554	586	615	641	669	705	764	776

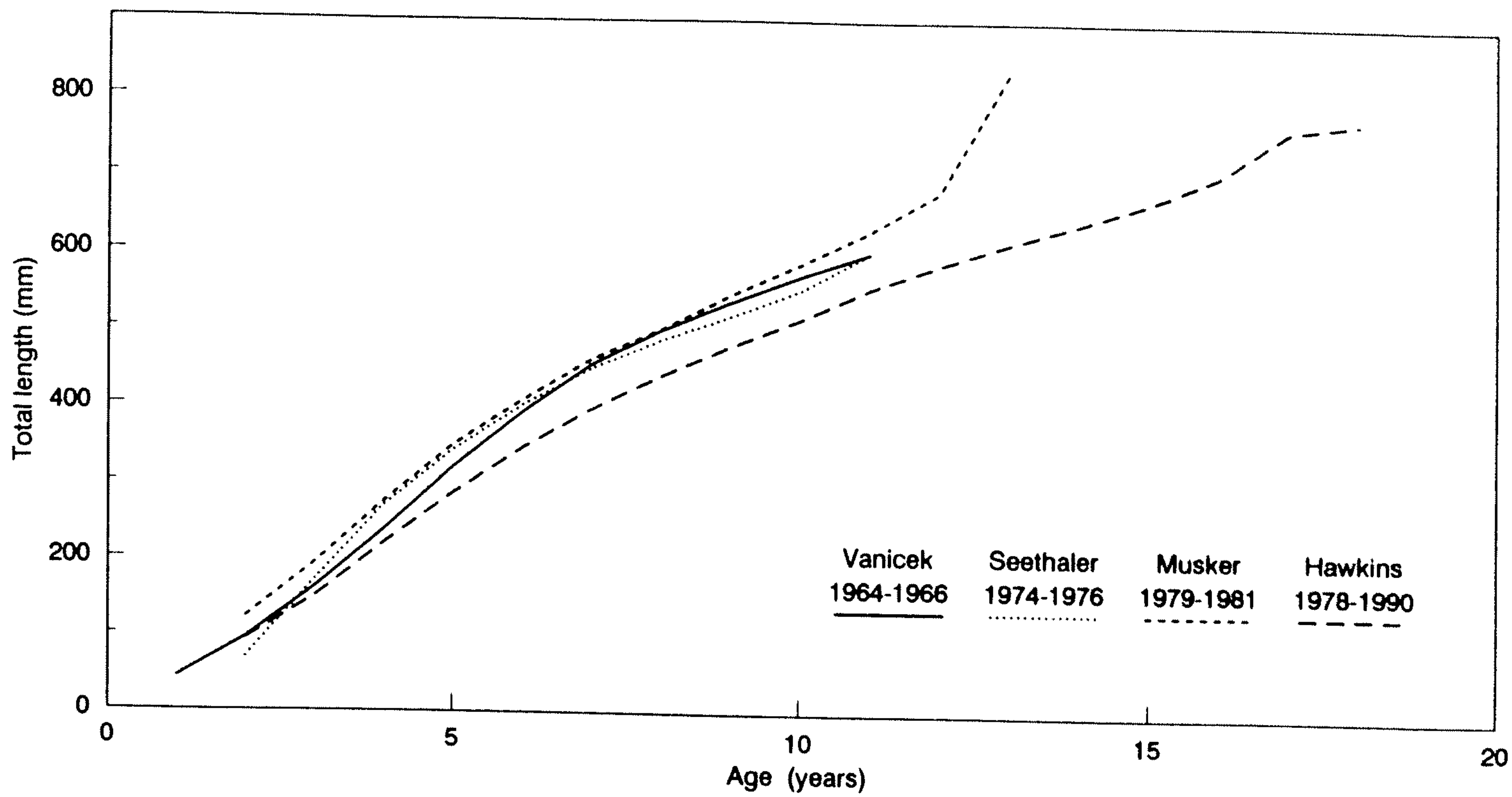

Figure 15. Comparison of average back-calculated lengths of Colorado squawfish from this and previous studies in the Upper Colorado River Basin.

Relative growth

Average annual growth increments were determined from estimated length at age (Tables 3-7). Growth increment between years was greatest (over 60 mm) between 3-4 or 4-5 years (Figure 16). Yearly growth decreased to about 30 mm per year after age 12, but tended to increase in later years (approximately at age 16). Annual relative growth decreased with age to between 5-10%, and fish over 12 years of age grew only about 6% of their body length (approximately 35 mm) each year (Figure 17). Annual relative growth of recaptured fish over 500 mm TL was only about 1-2% (approximately 10-15 mm) of body length each year (Figure 17). This may be evidence of a negative effect of tagging on fish growth. Growth of recaptured fish also exhibited a slight increase at larger sizes. The reason for this is unknown, although it was evidenced by both back-calculated and recaptured-fish data.

The highly variable growth obtained from scales of fish over 10 years old may be the result of inaccurate ages (Figures 14 and 16). If annuli were missed after age 10, then fish growth might appear greater than it actually is. Cui-ui grew rapidly during their first 10 years, slowly from 10 to 20 years, and very slowly after 20 years (Scoppettone 1988). Age and growth were correlated up to some age, possibly at sexual maturity, after which fish ceased growing. Age was less strongly correlated with size after cui-ui reached sexual maturity. Scoppettone (1988) noted that older fish tended to have larger heads

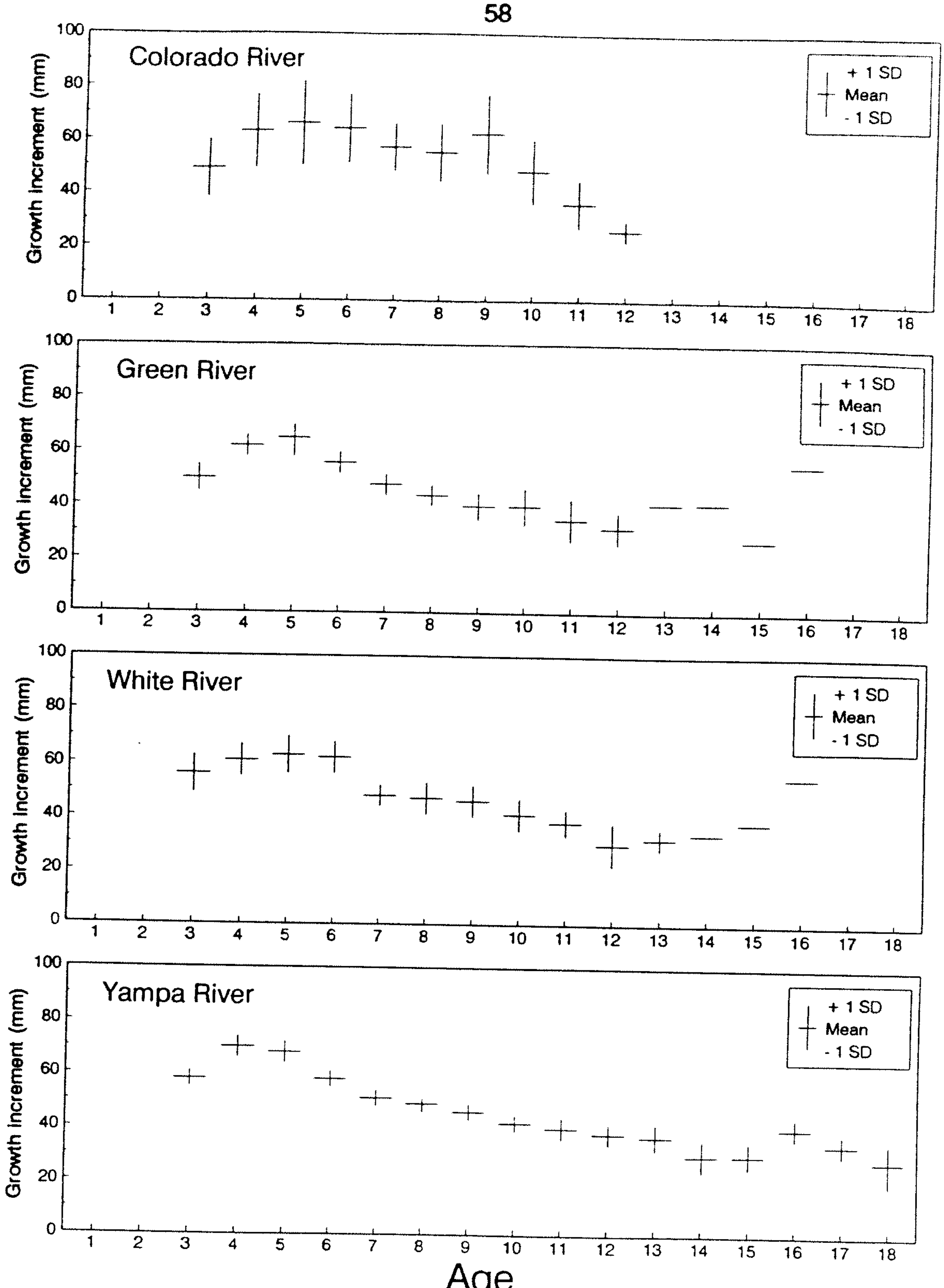

Figure 16. Average annual growth increment of Colorado squawfish from the Upper Colorado River Basin, 1978-1990. Vertical bars represent one standard deviation.

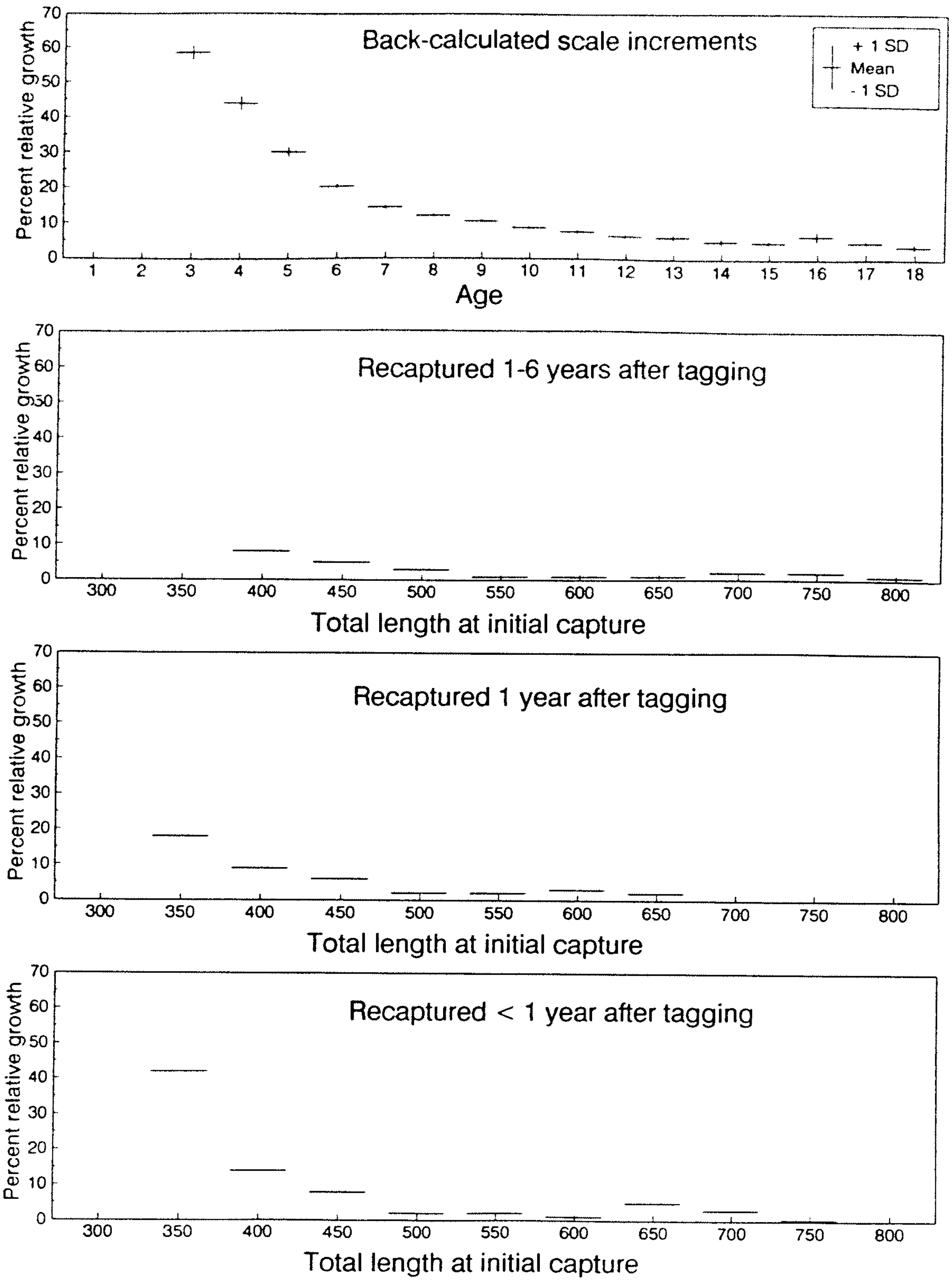

Figure 17. Annual relative growth of Colorado squawfish from the Upper Colorado River Basin, 1978-1990, based on back-calculated lengths and mark-recapture data.

than younger fish of the same size. Large Colorado squawfish of the same length also exhibit different head sizes.

Estimated scale ages are inaccurate in some fish after growth becomes asymptotic (Beamish and McFarlane 1987). Based on tag-recapture records, Colorado squawfish growth approached an asymptote after 500 mm TL, which is about 10 years old based on scale ages (Figure 17). Whether or not tagging affected growth is unknown. Average annual length increments of fish over 500 mm TL were greater than tag-recapture increments and did not approach the asymptote. At about 16 years of age, fish actually increased their yearly growth increment (Figure 16). This could have been due to inaccurate ages of older fish.

von Bertalanffy growth function

Unknown coefficients of the von Bertalanffy growth function were estimated from back-calculated lengths derived from scales (Tables 3-7). Walford plots were used to estimate asymptotic length (L_∞) based on back-calculated lengths (Figure 18). Asymptotic length approximated maximum length that fish in the population approach with increased age. Growth coefficient (K) and asymptotic length were compared for fish from rivers included in this and previous studies (Table 9). Lengths of Colorado squawfish from the Green River were estimated from von Bertalanffy growth curves using data from this and previous studies (Figure 19). Calculated growth rates were

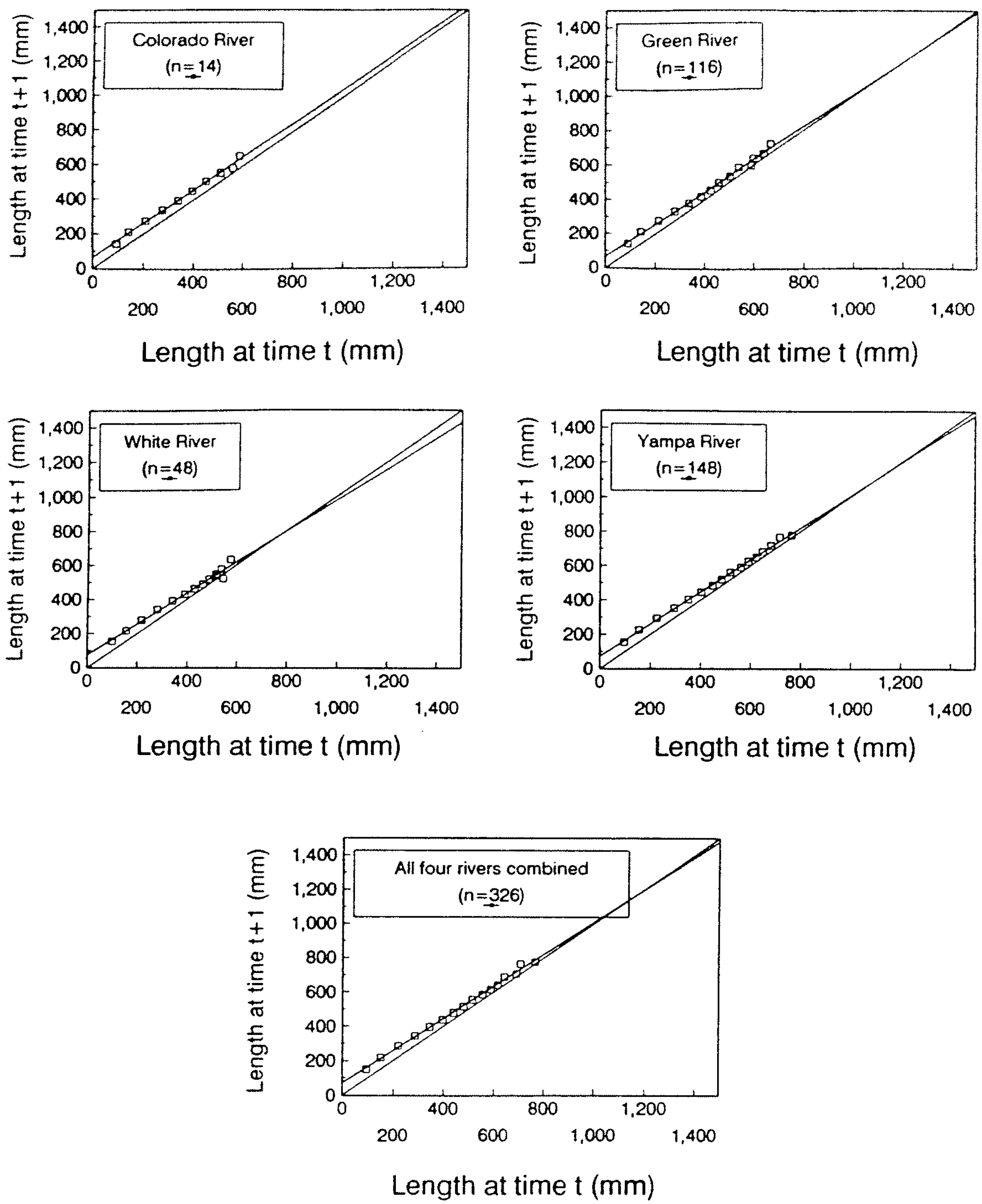

Figure 18. Walford plots based on back-calculated lengths of Colorado squawfish from the Upper Colorado River Basin, 1978-1990.

Table 9. Asymptotic length (L_∞) and von Bertalanffy coefficients K and t_o derived from Walford plots for Colorado squawfish from the Upper Colorado River Basin examined in this and previous studies. n = number of fish.

	n	L_∞ (mm)	K	t_o
Vanicek and Kramer (1969), 1964-1966:				
Green River	182	1144.	0.07475	0.64959
Seethaler (1978), 1974-1976:				
Green River	68	752	0.15767	1.29628
Musker (1981) adjusted, 1979-1981:				
Combined all rivers	139	1147	0.08611	1.01437
Hawkins, 1978-1990: *				
Green River	116	1246	0.05347	0.43075
White River	48	781	0.09543	0.25031
Yampa River	148	1221	0.06675	0.60655
Combined all rivers	326	1152	0.06293	0.58136

* Colorado River not included due to small sample size (n = 14).

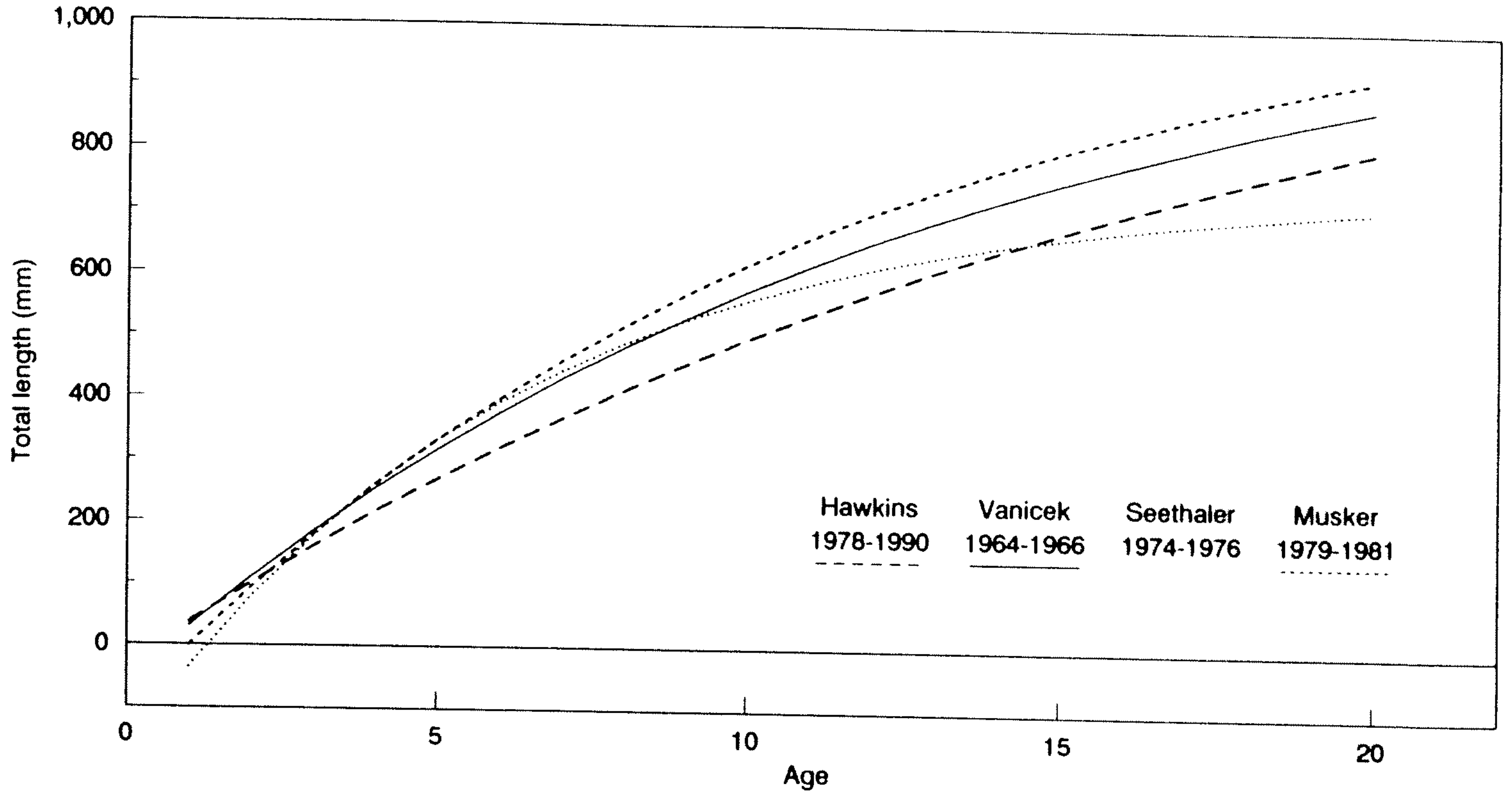

Figure 19. Comparison of calculated lengths at age from von Bertalanffy growth curves from this and previous studies of Colorado squawfish from the Green River.

apparently equal among all studies, but Seethaler's (1978) data suggested a lower asymptotic length (752 mm TL). The von Bertalanffy curves showed that I aged fish about one year older at a given size than Seethaler (1978), Vanicek and Kramer (1969), or Musker (1981).

RECOMMENDATIONS

Scales should be taken from each Colorado squawfish collected in the field, with greater effort to collect small fish (< 400 mm). In large samples of small fish, scales can be removed from a representative sample of each size group. Some small fish could be sacrificed to compare accuracy of ageing scales and other bony structures such as otoliths, opercula, or vertebrae. Hatchery-raised fish that are stocked in the wild should be marked with a unique, group mark to provide future known-age fish for age validation.

Work should continue with ageing scales, and otoliths, vertebrae, and opercula should also be aged. Ages from other bony structures may corroborate estimated scale ages by partial validation (Beamish and McFarlane 1983). Bony structures will not be readily available because of the rarity of the species, so any fish killed should be properly handled. Dead fish should be frozen or preserved in alcohol, not formalin since formalin decalcifies bone.

Acquisition and maintenance of capture records is extremely important. Increased caution and accuracy in measuring fish length and weight will provide better descriptive statistics. Measuring fish standard length will provide a better basis for calculating growth between captures because total length measurements are influenced by erosion of the caudal fin. Nonlethal techniques that identify sex of fish in the field should be developed and used to better characterize immature, male, and female segments of populations. Segregating sexes would improve estimates of length at age, weight-length relationship, and condition. Carlin tags used in the past probably negatively affected growth. Researchers in the Colorado River Basin have changed to small Passive Integrated Transponder (PIT) tags that are implanted subcutaneously. These new methods should be monitored to insure that their affect on fish growth is minimal.

SUMMARY

A total of 2176 Colorado squawfish was tagged between 1978 and 1989 in the Upper Colorado River Basin. Of the tagged fish, 279 were recaptured once, 42 were recaptured twice, and three were recaptured three times. Total lengths ranged 81-896 mm. Modal size groups were 500-600 mm TL for fish from the Colorado, Green, White, and Yampa rivers. All Colorado squawfish from the Yampa River were over 350 mm TL; most were over 450 mm TL, suggesting recruitment into the Yampa River after attaining sexual maturity. Yearly length-frequency distributions for fish from each river were similar each year suggesting continuous recruitment into the sampled adult population. Of 165 Colorado squawfish sexed, 130 (79%) were males.

Pooled, among months weight-length relationships for each river were:

Colorado River $\text{Log}_{10} W = -6.384 + 3.463 * \text{Log}_{10} L$,

Green River $\text{Log}_{10} W = -5.692 + 3.206 * \text{Log}_{10} L$,

White River $\text{Log}_{10} W = -5.555 + 3.156 * \text{Log}_{10} L$, and

Yampa River $\text{Log}_{10} W = -6.026 + 3.339 * \text{Log}_{10} L$,

where W is weight (g), and L is total length (mm). Weight-length relationships were very similar between Colorado River and Yampa River fish and between Green River and White River fish. Fish from the Colorado or Yampa rivers tended to be heavier at a given length than fish from the Green or White rivers. Colorado squawfish reached maximum relative condition in June, prior to

spawning, and a loss of condition occurred in July or August, probably as a result of migration or release of gametes at spawning.

A total of 336 scales was used to develop a body-length to scale-radius relationship. The relationship was best described by:

Fish length = 185.6358 scale radius + 45.1507.

Of 336 scales, 326 were aged and 10 were not because of several indistinct annuli. The first annulus was not observed on scales because scales had not formed or were newly formed as Colorado squawfish entered their first winter. After adjusting for the missing annulus, scales were suitable for ageing Colorado squawfish up to 10 years old. Older ages were obtained but not validated. The oldest fish was an 18-year-old from the Yampa River. Ages of oldest fish from the Green, White, and Colorado rivers were 16, 16, and 12 years, respectively. Scale ages were validated up to 10 years of age by correctly ageing two known-age, stocked fish that were recaptured as 10 year olds . Ages over 10 years may be accurate but are subject to an unknown amount of error. Additional validation of older ages with tagged and recaptured fish was partially successful. Relative growth calculated from lengths at tagging and recapture was lower than growth calculated from scales; this suggested either a detrimental tag affect or inaccurate estimated ages of older fish. Back-calculated lengths and von Bertalanffy growth curves were similar for fish up to age 7 or age 8, at which time growth rates varied between rivers.

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APPENDIX

Table A - 1. Back-calculated total lengths (TL) of 139 Colorado squawfish from the Upper Colorado River System, 1979-1981, from Musker (1981) data. Scale ages adjusted for missing first annulus and length-at-annulus recalculated based on new fish-length to scale-radius relationship.

			Mean estimated total length (mm) at annulus												
Age Group	n	Mean TL	1	2	3	4	5	6	7	8	9	10	11	12	13
I	-	-	-												
II	10	98	-	90											
III	5	189	-	132	177										
IV	5	307	-	116	190	274									
V	19	434	-	136	212	316	396								
VI	17	458	-	121	201	286	368	428							
VII	27	497	-	130	201	280	354	427	481						
VIII	31	516	-	122	187	258	327	397	461	505					
IX	11	576	-	122	178	252	327	393	453	508	557				
X	6	602	-	120	190	269	340	411	454	505	555	598			
XI	5	630	-	120	177	239	299	347	407	457	517	567	616		
XII	2	647	-	118	173	228	291	354	407	462	506	556	606	629	
XIII	1	879	-	108	167	233	296	362	403	506	597	669	738	782	848
Mean			-	123	194	275	349	407	461	500	546	586	629	680	848
95% CI			-	4	6	9	11	11	12	16	24	33	49	101	0
n			-	139	129	124	119	100	83	56	25	14	8	31	1

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