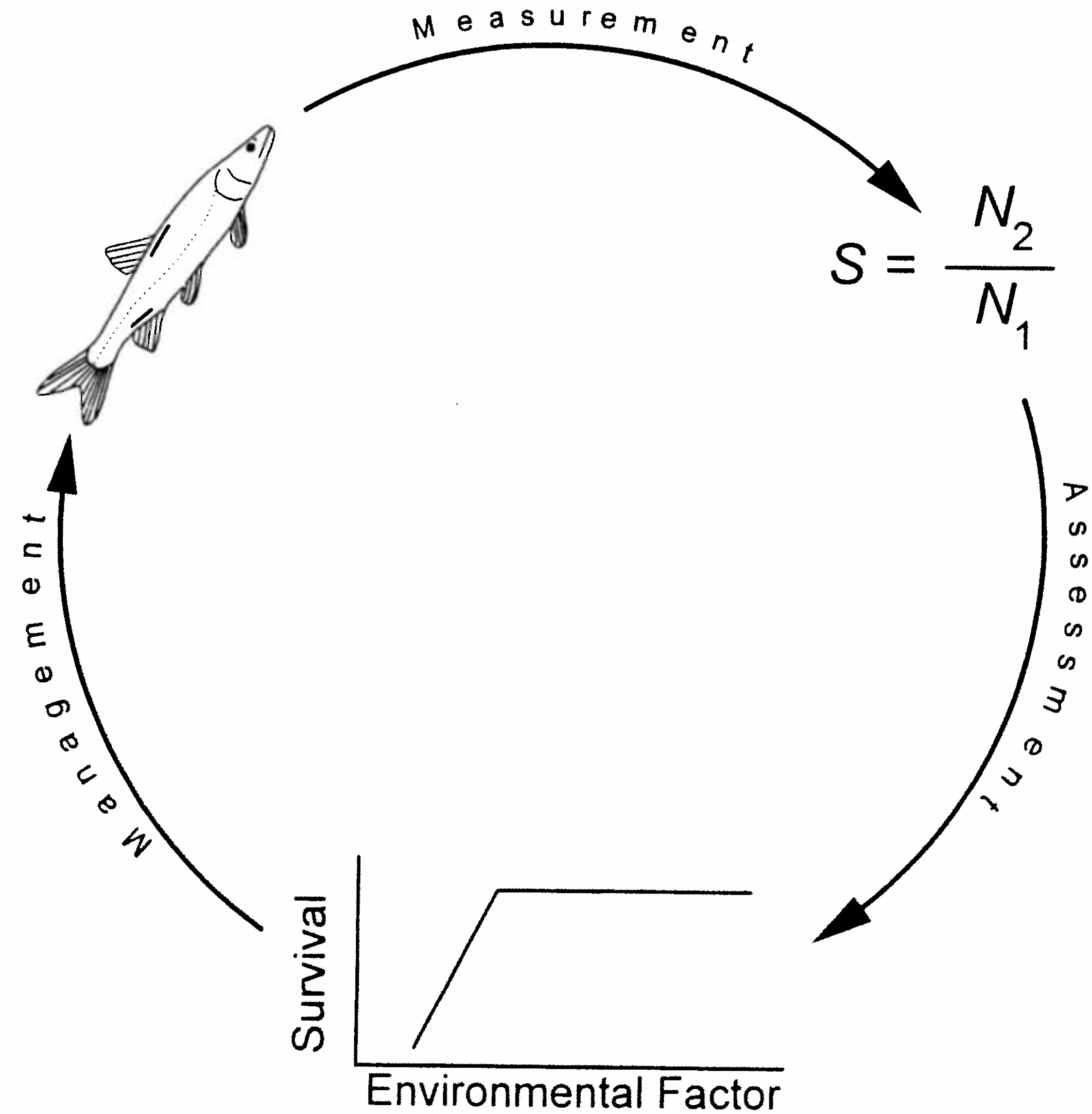
Estimation Of Winter Survival, Movement, And Dispersal Of Young Colorado Squawfish In The Green River, Utah



Estimation of Winter Survival, Movement and Dispersal of Young Colorado Squawfish in the Green River, Utah

Recovery Program Project 36

Final Report

G. Bruce Haines[1], Daniel W. Beyers[2], and Timothy Modde[1]

[1]U. S. Fish and Wildlife Service,

Colorado River Fishery Project,

266 West 100 North, Vernal, Utah 84078

[2]Larval Fish Laboratory,

Department of Fishery and Wildlife Biology,

Colorado State University, Fort Collins, Colorado 80523

27 July 1998

Contribution 96 of the Larval Fish Laboratory, Department of Fishery and Wildlife Biology,

Colorado State University

Acknowledgments

We are grateful to J. M. Bundy, Colorado State University Larval Fish Laboratory, T. Hatch and numerous technicians of the Colorado River Fish Project, U. S. Fish and Wildlife Service, for their diligence in the field. K. R. Bestgen facilitated our use of his unpublished data and provided constructive comments throughout the course of the investigation. We thank Kevin Bestgen, Chuck McAda, Tom Chart, and Robert Forrest for their thoughtful reviews. This study was funded by the Recovery Implementation Program for the Endangered Fish Species in the Upper Colorado River Basin. The Recovery Program is a joint effort of the U.S. Fish and Wildlife Service, U.S. Bureau of Reclamation, Western Area Power Administration, states of Colorado, Utah, and Wyoming, Upper Basin water users, environmental organizations, and the Colorado River Energy Distributors Association.

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Colorado squawfish, population estimates, winter survival, capture-recapture, catch per unit effort, age-0, age-1

Executive Summary

Population estimates for age-0 and age-1 Colorado squawfish in two 32-km reaches of the Green River were made using capture-recapture procedures. Comparisons of autumn and spring population estimates were used to assess overwinter survival and evaluate factors that affect it. Previous research using traditional methodology has demonstrated that estimates obtained using catch per unit effort (CPUE) are unreliable for assessing overwinter survival. Capture-recapture provides a more rigorous basis for estimating abundance of young Colorado squawfish because it can account for variable capture probabilities.

Objectives of this study were to employ capture-recapture methods to (1) compare estimates of abundance from capture-recapture and CPUE methods; (2) estimate overwinter survival of age-0 Colorado squawfish; (3) estimate seining catchability coefficients for autumn and spring sampling; (4) determine extent of downstream movement of marked Colorado squawfish between 1 November and 1 April; and (5) determine the effect of timing and magnitude of spring flows on dispersal of age-1 Colorado squawfish.

We found little evidence that abundance estimates from CPUE accurately reflect the number of young Colorado squawfish in study reaches in the Green River. There was only a weak correlation ($r = 0.50$, $P = 0.14$) between estimates of abundance from CPUE and capture-recapture. On several occasions, CPUE estimates had precision that was comparable to that achieved with capture-recapture, but the estimates differed by as much as 217%. Inaccuracy and greater variability of CPUE was attributed to effects of water temperature on capture probability. Evidence suggests that young Colorado squawfish are less likely to be caught when water temperatures are cool, regardless of their abundance.

Overwinter survival probabilities of age-0 fish ranged from 0.06 to 0.62. Three of four estimates were similar and ranged from 0.56 to 0.62. Low overwinter survival (0.06) during 1995-1996 may have been due to small size of age-0 fish in autumn or relatively high winter discharge.

Recaptures of marked age-0 and age-1 Colorado squawfish showed that they moved less than 16 km downstream during sampling periods that ranged from 2 to 21 days. Similarly, age-0 fish that were marked in autumn and recaptured the following spring moved less than 16 km

downstream after being at large for 170 to 200 d. The role of spring flooding in redistribution of age-1 Colorado squawfish remains unclear because few fish were captured during post-runoff surveys conducted in July and August.

Introduction

The Colorado squawfish *Ptychocheilus lucius* is a large piscivorous cyprinid once abundant in major tributaries throughout the Colorado River basin. It has, however, been extirpated throughout much of its historic range following conversion of riverine habitat to artificial impoundments, construction of migratory barriers, and introduction of nonnative fishes (Tyus 1991a). The largest remaining populations of Colorado squawfish exist in the Green River subbasin (Tyus 1991a), which is the least impacted of the large tributaries of the Colorado River. Although the adult population in the Green River subbasin appears stable and persistent (McAda et al. 1994), survival of young fish in nursery habitats composed of low velocity shoreline embayments and backwaters is variable (Tyus 1991a; Tyus and Haines 1991) and may be influenced by upstream releases from Flaming Gorge Dam (Carlson and Muth 1989; Valdez and Cowdell 1996). The closure of Flaming Gorge Dam on the Green River in 1962 and its subsequent operation is one potential cause of variable recruitment (Carlson and Muth 1989; U.S. Fish and Wildlife Service 1992). In 1992 the U.S. Fish and Wildlife Service issued a Biological Opinion (U. S. Fish and Wildlife Service 1992) that recommended discharge patterns from Flaming Gorge Dam that more closely mimic the pre-impoundment hydrograph of the Green River. Because little was known about the effects of winter and spring flows on young Colorado squawfish the recommendations for winter and spring flows were largely based on knowledge of adult Colorado squawfish. In 1992 the U.S. Bureau of Reclamation initiated the *Five-Year Flaming Gorge Research Program* (Crist and Williams 1994), which proposed to evaluate biological and physical responses of the Green River ecosystem to recommended flows and obtain information about the effects of winter and spring flows on endangered fishes.

Several studies in the *Five-Year Flaming Gorge Research Program* emphasized study of effects of environmental conditions on young-of-year Colorado squawfish. One study (Valdez and Cowdell 1996) estimated overwinter survival of young-of-year Colorado squawfish by measuring relative densities (individuals/100-m^2 seined) in autumn and the following spring based on catch per unit effort (CPUE). This method assumed that fish were equally vulnerable (i.e., same probability of capture) to seining in the autumn and spring and that the same population was sampled on both occasions. Tyus and Haines (1991) used a similar method and reported that estimates based on seine CPUE were unreliable for assessing overwinter survival. They concluded that a likely explanation for poor performance of the seine-CPUE method was that capture vulnerability varied on each sampling occasion. Haines and Modde (1996) demonstrated that capture-recapture provided a more rigorous basis for estimating abundance of young Colorado squawfish because it accounted for variable capture probabilities.

The objectives of this study were to employ the capture-recapture methodology used by Haines and Modde (1996) in two 32-km reaches of the Green River in order to (1) compare estimates of Colorado squawfish abundance from capture-recapture and CPUE methods; (2) estimate overwinter survival of age-0 Colorado squawfish; (3) estimate seining catchability coefficients (probability of capture per seine haul; Ricker 1975) for autumn and spring sampling; (4) determine extent of downstream movement of marked Colorado squawfish between 1 November and 1 April; and (5) determine the effect of timing and magnitude of spring flows on dispersal of age-1 Colorado squawfish. Results were used to evaluate compliance with assumptions of capture-recapture methodology, examine the advantages and disadvantages of capture-recapture and CPUE, and evaluate evidence that links overwinter survival with discharge magnitude, discharge variability, or fish size.

Study Area

The Green River originates in western Wyoming and flows into northeastern Utah where it is impounded by Flaming Gorge Dam (Figure 1). From Flaming Gorge Dam, the river flows unimpeded for 655 km through eastern Utah and northwestern Colorado to its confluence with the Colorado River. Our study sites were located within two low gradient river reaches (RK 0-193 and RK 321-513) known to be important nursery areas for young-of-year Colorado squawfish (Tyus and Haines 1991; McAda et al. 1994). These low gradient (0.2-0.4 m/km), alluvial reaches of the Green River consist predominantly of sand and silt substrates (Haines and Tyus 1990; Tyus and Haines 1991; McAda et al. 1994). One 32-km capture-recapture study site was located within each nursery reach; the exact location within each reach was based on ease of access and avoidance of concurrent nursery habitat study areas. The downstream study site was in Canyonlands National Park (RK 44-76). This site was studied during autumn and spring of 1994-1995 and 1995-1996. The upstream site was near Jensen, Utah (RK 451-483). It was studied for three years 1992-1993, 1993-1994, and 1994-1995. The first year (1992-1993) was a pilot-scale study and the study reach was 16-km long (RK 467-483).

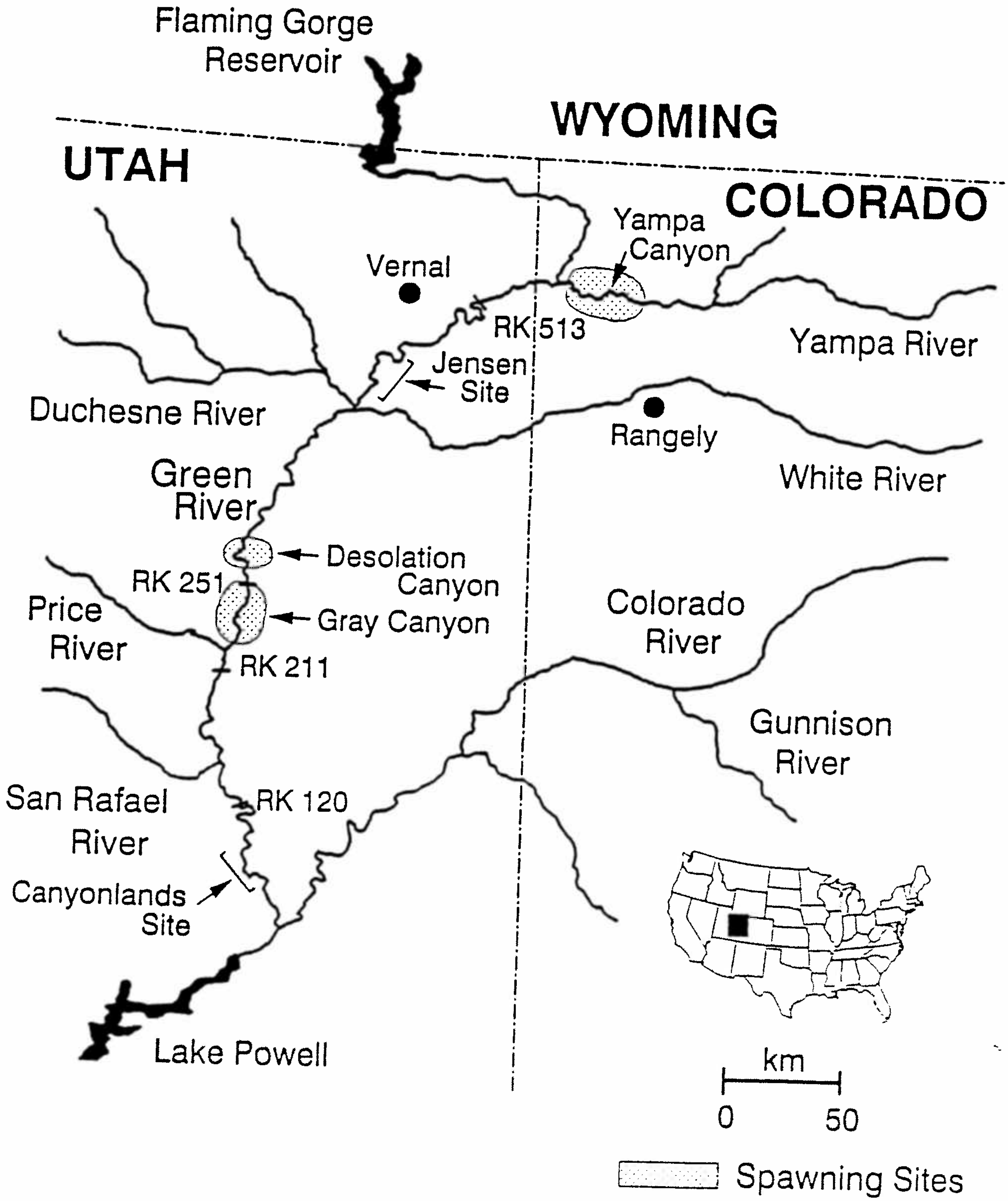

Figure 1. Green River study area.

Methods

Capture-Recapture Population Estimates

Fish capture and marking. - The abundance of young-of-year Colorado squawfish in autumn and the following spring was estimated using capture-recapture population estimation methods (Otis et al. 1978; Seber 1982; Haines and Modde 1996). Study sites were sampled on three occasions (passes) for each population estimate. A pass consisted of seining all backwaters with surface area ≥ 3 m^2 within each study reach. Seines were 4.5-m long × 1.9-m deep with 4.0-mm bar mesh. The area seined was generally between 70 and 100% of the of the total surface area. In the Jensen reach, however, a few backwaters were large and deep and only about 50% of the total area could be seined. The number of seine hauls per backwater averaged 2-3 for the Canyonlands reach and ranged from 1 to 6; the backwaters in the Jensen reach were somewhat larger and the number of seine hauls per backwater averaged 3-5 and ranged from 1 to 23. The backwaters were not blocked prior to seining. Colorado squawfish were marked on the first two passes but not on the third, with one exception: in autumn 1992 fish were marked only on the first pass. Dates of each sampling pass are given in Appendix 1.

Captured Colorado squawfish < 100-mm total length (TL) were anesthetized with 0.1 g/L MS-222 and marked with syringe-injected elastomer (Northwest Marine Technology, Shaw Island, Washington). Approximately 100 fish (if available) were selected at random and measured (TL) during each population estimate. Fish were allowed to recover in a 20-L pail of river water for 20 to 30 min while seining, marking, and data collection were completed. Marked fish were released into backwaters where they were captured. On seven occasions postmarking survival was estimated by retaining marked fish overnight (18 to 19 h) in a floating enclosure.

Captured Colorado squawfish > 100 mm TL were not considered part of the age-0 cohort. These fish were measured (TL), marked with internally implanted passive integrated transponder (PIT) tags (Prentice et al. 1990) and released back into the same backwater.

Parameter estimates. - Population estimates were calculated using the computer program CAPTURE (White et al. 1982) assuming closed capture-recapture models (Otis et al.

1978). These models give maximum likelihood estimates of population size and probability of capture for each sampling occasion. Population estimates were transformed to densities (capture-recapture estimate / study-reach length) to allow comparison of estimates made during the first year of this project (16-km reach) with subsequent years (32-km reaches).

Overwinter survival probability $(\hat{S})$ was calculated by dividing each spring population estimate $(\hat{N}_2)$ by the estimate for the previous autumn $(\hat{N}_1)$:

$$\hat{S} = \frac{\hat{N}_2}{\hat{N}_1} .$$

Variance of S was calculated by the delta method for propagation of errors (Robson and Spangler 1978):

$$\hat{V}(\hat{S}) = \left(\frac{1}{\hat{N}_1}\right)^2 \hat{V}_2(\hat{N}_2) + \left(\frac{\hat{N}_2}{\hat{N}_1^2}\right)^2 \hat{V}_1(\hat{N}_1) .$$

Comparison of CPUE and Capture-Recapture Estimates

The same capture data used to calculate capture-recapture estimates were also used to estimate CPUE. Catch per unit effort for a backwater was defined as the number of Colorado squawfish captured per seine haul. To explore the effect of effort on CPUE estimates, CPUE was calculated for a single pass and for combined sampling passes. Catch per unit effort for a single pass was estimated by averaging CPUE of each backwater for that pass. Combined CPUE was calculated by averaging CPUE of each backwater from all three passes.

Estimates of abundance and overwinter survival from CPUE and capture-recapture were compared by inspection and by testing for an association between the measures. Pearson correlation coefficient was used to evaluate the association between CPUE and population density (Zar 1984).

Overwinter survival estimates derived by dividing CPUE in the spring by CPUE in the autumn assumes that the fish are equally vulnerable to capture in the spring and autumn. To test this relationship, we calculated seining catchability coefficients. Seining catchability coefficient for a sampling pass was defined as the probability that a Colorado squawfish would be caught per seine haul (Ricker 1975). Seining catchability coefficient was calculated by dividing the probability of capture for a sampling pass (derived from CAPTURE) by the number of seine hauls in that pass. This measure accounts for the effect of variable effort so that catchability coefficients from different sites and occasions can be compared. The difference between autumn and spring catchability coefficients were compared by calculating a *t*-statistic and comparing it to a two-tailed Student's critical value. Pearson correlation coefficient with Bonferroni adjustment (Zar 1984) was used to evaluate the association between catchability coefficients and three measures of water temperature: main channel, backwater, and the difference between backwater and main channel temperature.

To compare variability of overwinter survival estimates from CPUE and capture-recapture methods, the coefficient of variation (CV) was computed. The CV is defined as (standard error of the estimate * 100)/mean). Coefficients of variation allow equitable comparison of precision among estimates with differing means because variance is expressed as a percent of the mean (Zar, 1984). Statistical analyses were conducted with SYSTAT software (Wilkinson 1990).

Movement

Marked Colorado squawfish were also used to study movement patterns. The 32-km study reaches were divided into 8-km sections. By varying mark location and color, fish were given a unique mark that identified which study section they were captured in. When a fish was recaptured, the marks allowed identification of the section where that individual fish was originally captured and the number of days at large.

To determine how annual spring flooding redistributed young Colorado squawfish, surveys were conducted in late July or early August to search for marked fish. Surveys began at the upstream boundary of each study reach and extended downstream 76 km for the Canyonlands site (RK 0 to 76) and 135 km for the Jensen site (RK 348 to 483). All backwater habitats were seined (70 to 100% of total backwater area) during these surveys. The Canyonlands reach was not sampled after runoff in summer 1996 because only 29 fish were marked during spring and it was unlikely that they would be recaptured.

In addition to our sampling, other fishery investigators also recorded captures of marked fish. Studies that were coincident with our investigations were *Interagency Standardized Monitoring Program* (ISMP), *Colorado Squawfish Nursery Habitat Availability, and Overwinter Survival of Age-0 Colorado Squawfish in the Green and Colorado Rivers*, and *Sampling for Larval Razorback Sucker in Canyonlands National Park and Glen Canyon National Recreation Area*.

Factors that Influence Overwinter Survival

A variety of factors may influence overwinter survival of age-0 Colorado squawfish. Two factors related to operation of Flaming Gorge Dam are variability and magnitude of discharge in the Green River during winter. To evaluate potential importance of these variables, graphical plots were constructed that depict survival probability as a function of average daily discharge and its CV during winter. Inspection of U.S. Geological Survey discharge records for the Green River near Jensen, Utah, suggested that the period from 1 October to 28 February was relatively stable and not influenced by spring runoff events (Figure 2); thus this interval was defined as the winter period. Overwinter survival probabilities for the Canyonlands and Jensen sites were plotted as functions of CV and mean discharge. Discharge data were obtained from U.S. Geological Survey records (provisional) from the Green River (gage number 09315000; Canyonlands site) and Jensen (gage number 09261000), Utah, gaging stations.

Size and energy reserves at the beginning of winter are biological factors that may influence overwinter survival of age-0 Colorado squawfish (Shuter and Post 1990; Thompson et al. 1991). Total length was used as a measure of size and energy reserves. We attempted to record TL of at least 100 young Colorado squawfish from each study site on each autumn or

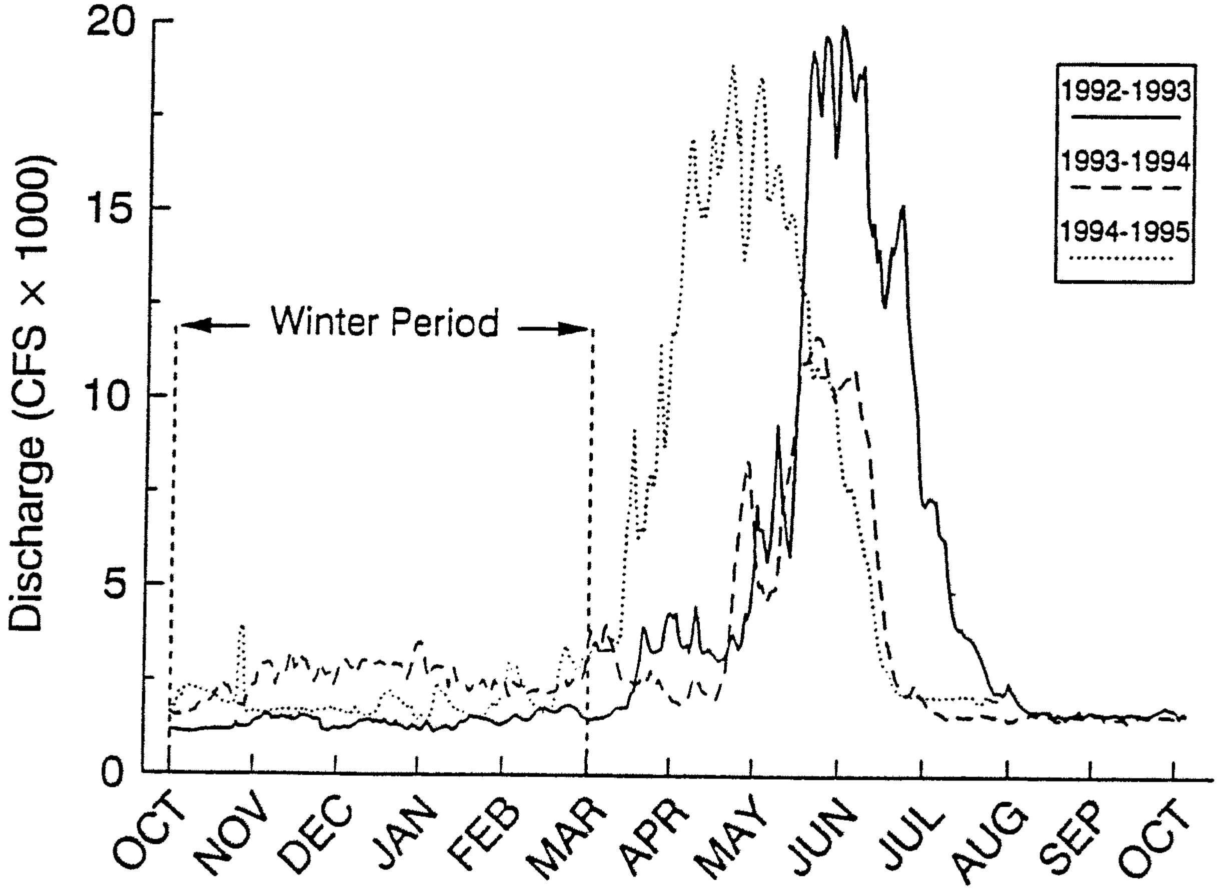

Figure 2. Illustration of mean daily discharge for the Green River near Jensen, Utah. The winter period is 1 October to 28 February.

spring sampling occasion. This objective was not always achieved due to scarcity of fish on some occasions. For occasions when sufficient data were collected, length-frequency plots were constructed. Overwinter survival probabilities at Canyonlands and Jensen sites were plotted as a function of the TL in autumn.

Results

Movement

Young Colorado squawfish moved only short distances during autumn and spring sampling periods. Of 112 fish marked and recaptured in autumn, 111 remained within the 8-km sections where they were originally marked; one fish moved downstream to an adjacent section. Of 76 fish marked and recaptured in spring, all were caught in sections where they were originally marked. Recaptured fish were at large for 2 to 21 d.

Twenty-six fish recaptured in spring were marked the previous autumn. Of these, 19 were captured in sections where they were originally marked, 6 were in adjacent downstream sections, and 1 was recaptured two sections upstream (7.4 km). These fish had been at large 170 to 200 d.

Eight fish marked in autumn 1994 in the Canyonlands reach were recaptured the following summer by researchers involved in the investigation entitled *Sampling for Larval Razorback Sucker in Canyonlands National Park and Glen Canyon National Recreation Area* (R. T. Muth, pers. comm.). Three fish were captured in sections where they were originally marked, two were in adjacent downstream sections, and three had moved two sections downstream. These fish had been at large for 246 to 263 d and were recaptured in June just before peak runoff. No other marked fish were captured by other fishery investigators. Sampling dates for other fishery investigators that collected age-0 and age-1 Colorado squawfish ranged from March to October 1993-1996, and sampling locations included upstream, within, and downstream of our study sites (Table 1).

Relatively few age-1 Colorado squawfish were captured during post-runoff surveys conducted in July and August. In the Jensen reach, 15 age-1 fish were captured on 18-20 July 1994 (32 backwaters sampled with 121 seine hauls); none of these fish were marked. No

Table 1. - Summary of other fishery investigations that collected age-0 and age-1 Colorado squawfish by seining in backwater habitats in the Green River 1993-1996.

Year	Dates	Location (RK)	Sampling program
1993	Mar 29- Apr 01	0-193	Overwinter survival
	Apr 04-06	405-422	Nursery habitat
	Aug 11-13	405-422	Nursery habitat
	Sep 21-29	0-193	ISMP
	Sep 27-29	338-515	ISMP
	Sep 30- Oct 01	405-422	Nursery habitat
1994	Mar 21-24	0-193	Overwinter survival
	Apr 05-07	405-422	Nursery habitat
	Jun 14-17	229-302	Nursery habitat
	Jul 21-24	229-302	Nursery habitat
	Aug 02-05	405-422	Nursery habitat
	Aug 17-21	229-302	Nursery habitat
	Sep 14-18	229-302	Nursery habitat
	Sep 20-23	0-193	ISMP
	Sep 27-30	405-422	Nursery habitat
	Oct 05-07	338-515	ISMP
1995	Mar 20-23	0-193	Overwinter survival
	Mar 28-31	405-422	Nursery habitat
	Apr 05-09	229-302	Nursery habitat
	Jun 04-23	45-55	Razorback monitoring
	Aug 10-14	229-302	Nursery habitat
	Aug 22-24	405-422	Nursery habitat
	Sep 14-18	229-302	Nursery habitat
	Sep 19-22	0-193	ISMP
	Sep 26-28	338-515	ISMP
	Oct 03-06	229-302	Nursery habitat
1996	Mar 14-17	0-193	Overwinter survival
	Mar 26-27	405-422	Nursery habitat
	Apr 18-20	229-302	Nursery habitat
	Jul 15-19	229-302	Nursery habitat
	Aug 06-09	405-422	Nursery habitat
	Aug 16-20	229-302	Nursery habitat
	Sep 10-12	405-422	Nursery habitat
	Sep 16-20	229-302	Nursery habitat
		0-193	ISMP
	Oct 01-03	338-515	ISMP

Colorado squawfish were captured on 7-10 August 1995 (23 backwaters sampled with 82 seine hauls). In the Canyonlands reach, 25 age-1 fish were captured on 1-4 August 1995 (60 backwaters sampled with 163 seine hauls). One fish marked during autumn was recaptured on 2 August 1995 approximately 10-km downstream of the section where it was originally captured.

Population and Survival Estimates

Fish capture and marking. - A total of 3,779 young Colorado squawfish were captured; 2,478 were marked and released; and 188 were recaptured (Appendix 1a-e). All backwaters were seined in each study reach. The number of backwater and low-velocity habitats seined per sampling pass ranged from 9 to 33 (mean = 19.9) for the Jensen reach and 17 to 52 (mean = 36.6) for the Canyonlands reach. The numbers of backwaters varied from year to year because of variations in discharge and the geomorphology processes that form backwaters; numbers varied from pass to pass primarily because small variations in discharge dewatered some habitats and flooded others. In most cases, however, the largest and deepest backwaters, where most of the young Colorado squawfish were captured, persisted from pass to pass. The Jensen reach had cooler water temperatures and more inclement weather during sampling compared to the Canyonlands reach. The number of days required to complete a three-pass population estimate ranged from 6 to 33 d for the Jensen reach and 6 d for the Canyonlands reach.

Survival of marked fish held overnight in enclosures averaged 85% (Table 2). The enclosures themselves were the source of some mortality. On one occasion small fish were entangled in the mesh of the enclosure, and on another it was suspected that sediment deposition and abrasion caused by wind turbulence may have resulted in mortalities.

Juvenile fish ranging from 100 to 230-mm TL were also caught in seine samples. In the Jensen reach, four juveniles were caught in 1994; none were caught in 1995. Ninety-six juveniles were captured in the Canyonlands reach in 1995 and three in 1996.

Size. - Length-frequency histograms for young Colorado squawfish showed that size in autumn varied yearly (Figures 3-6). Growth of age-0 fish at the Canyonlands site in

Table 2. - Summary of survival of young Colorado squawfish marked with syringe injected elastomer and held overnight (18-19 h) in enclosures in the Green River.

Date	Location (RK)	Mark	Number marked	Number survive	Survival (%)
20 Apr 94	464.2	rt dors, ant	20	19	95
5 Oct 94	63.6	lt dors, ant	34	34	100
23 Mar 95	64.4	rt dors, ant	22	19	86[a]
25 Mar 95	64.3	rt dors, pos	8	8	100
11 Oct 95	55.2	lt dors, pos	10	1	10[b]
20 Apr 96	50.2	rt dors, pos	9	6	67
22 Apr 96	50.2	rt dors, pos	5	5	100
			108	92	85[c]

[a]Dead fish were smaller than survivors and had marks on their abdomens; cause of death was probably due to entanglement in enclosure mesh.
[b]Handling conditions seemed good; afternoon wind may have caused turbulence that resulted in sedimentation of enclosure and mortality
[c] mean calculated as (92 /108) * 100

summer 1994 was surprisingly high. The distribution of total lengths for fish captured in the Canyonlands reach that year was bimodal with modes at 47 and 67 mm (Figure 5). Analysis of drift collections from the Green River near Green River, Utah, showed that emergence of larval Colorado squawfish also had a bimodal distribution for summer 1994 (K. R. Bestgen, pers. comm.). Emergence periods were concentrated around 28 June and 25 July. To confirm that age-0 Colorado squawfish can attain the observed sizes in their first season, a growth analysis was conducted. The analysis simulated growth of age-0 Colorado squawfish using (1) estimated fertilization date based on emergence periods (15 June), (2) a temperature-dependent growth equation (Bestgen 1996; Bestgen et al. 1997), (3) the temperature regime for the Green River near Green River based on U.S. Geological Survey records for summer 1994, (4) an average daily growth rate of 0.5-mm TL/d which is a common growth rate in wild Colorado squawfish (Bestgen 1996), and (5) day of capture for marking as the end of the growth period. Results of

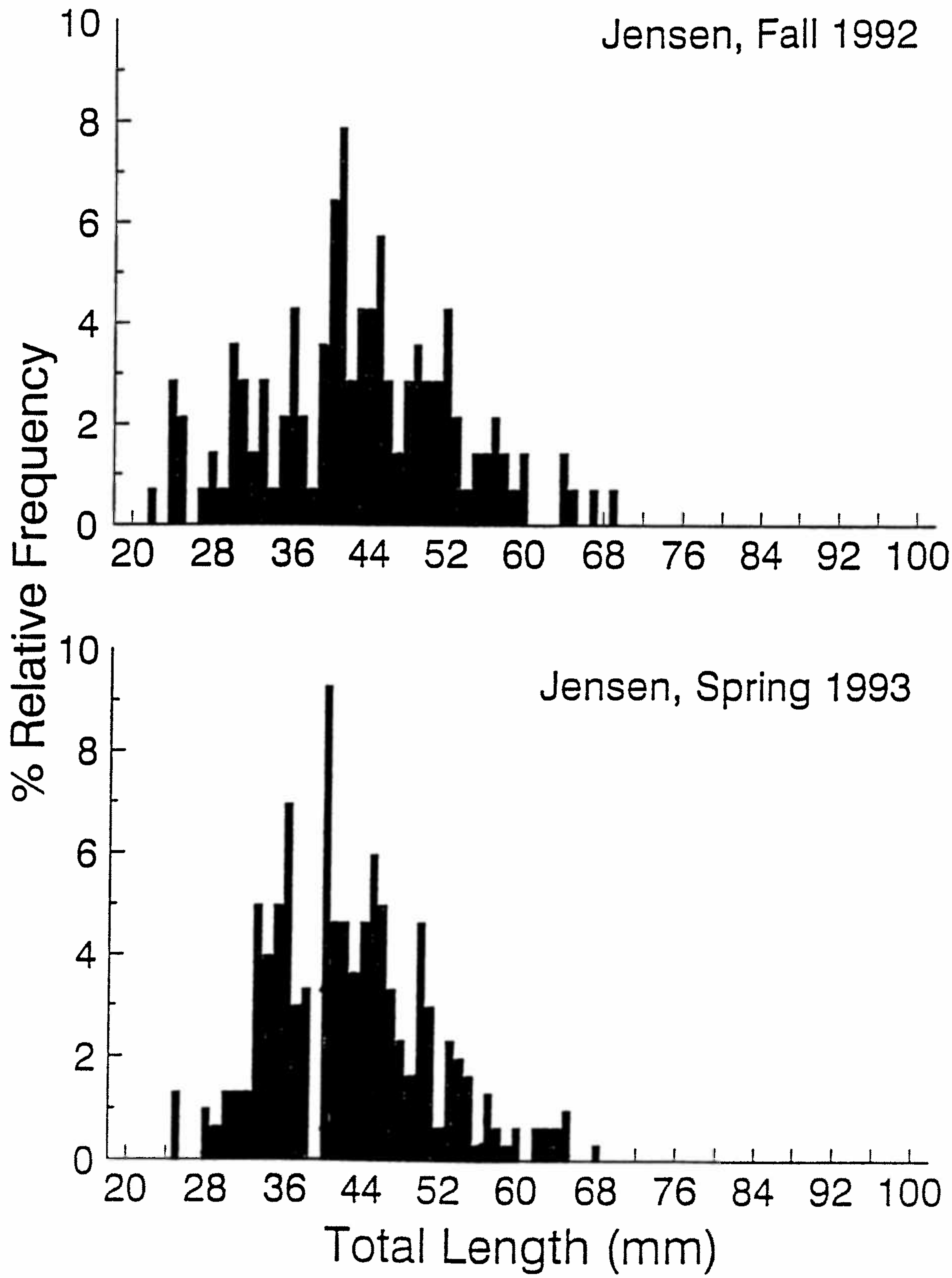

Figure 3. Length-frequency histograms for age-0 and age-1 Colorado squawfish in the Green River near Jensen, Utah, autumn 1992 and spring 1993.

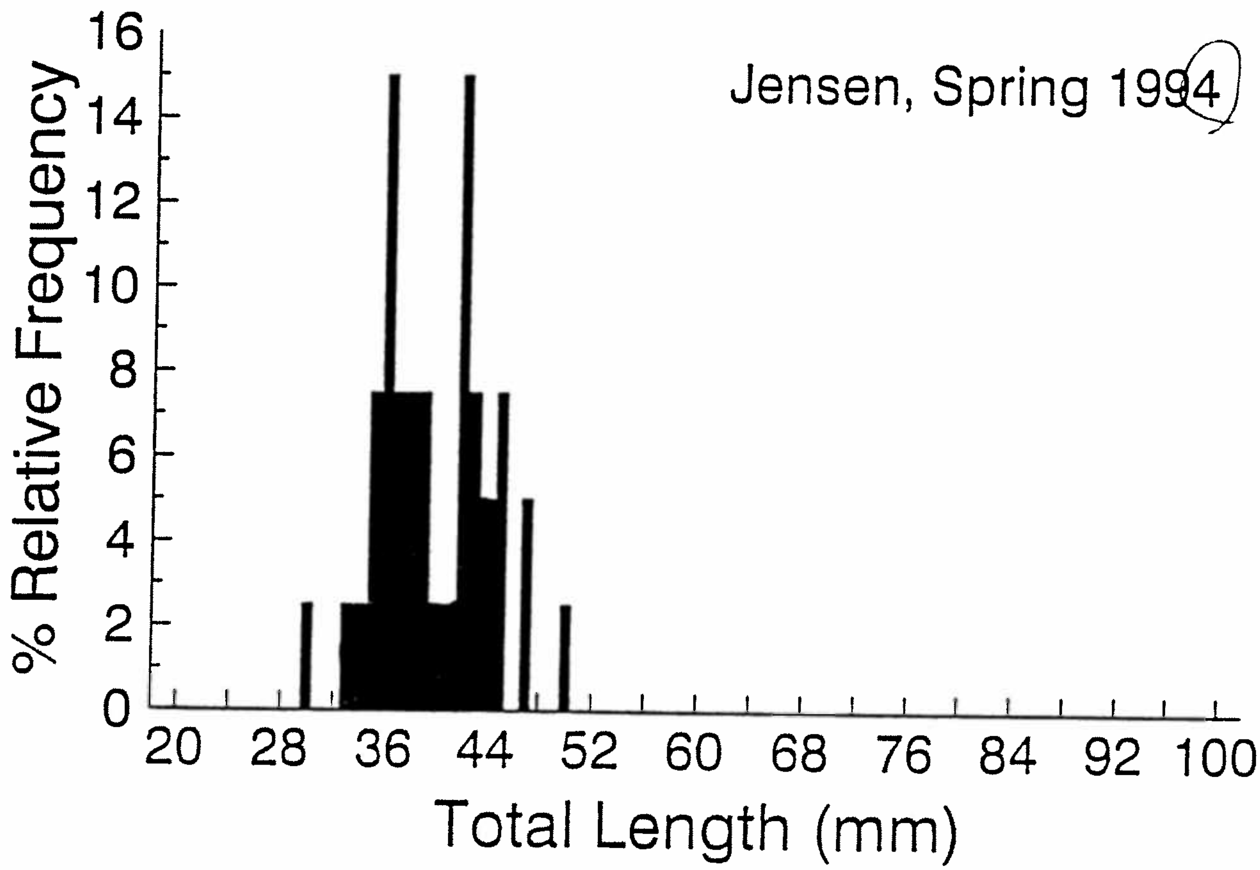

Figure 4. Length-frequency histogram for age-1 Colorado squawfish in the Green River near Jensen, Utah, spring 1993.

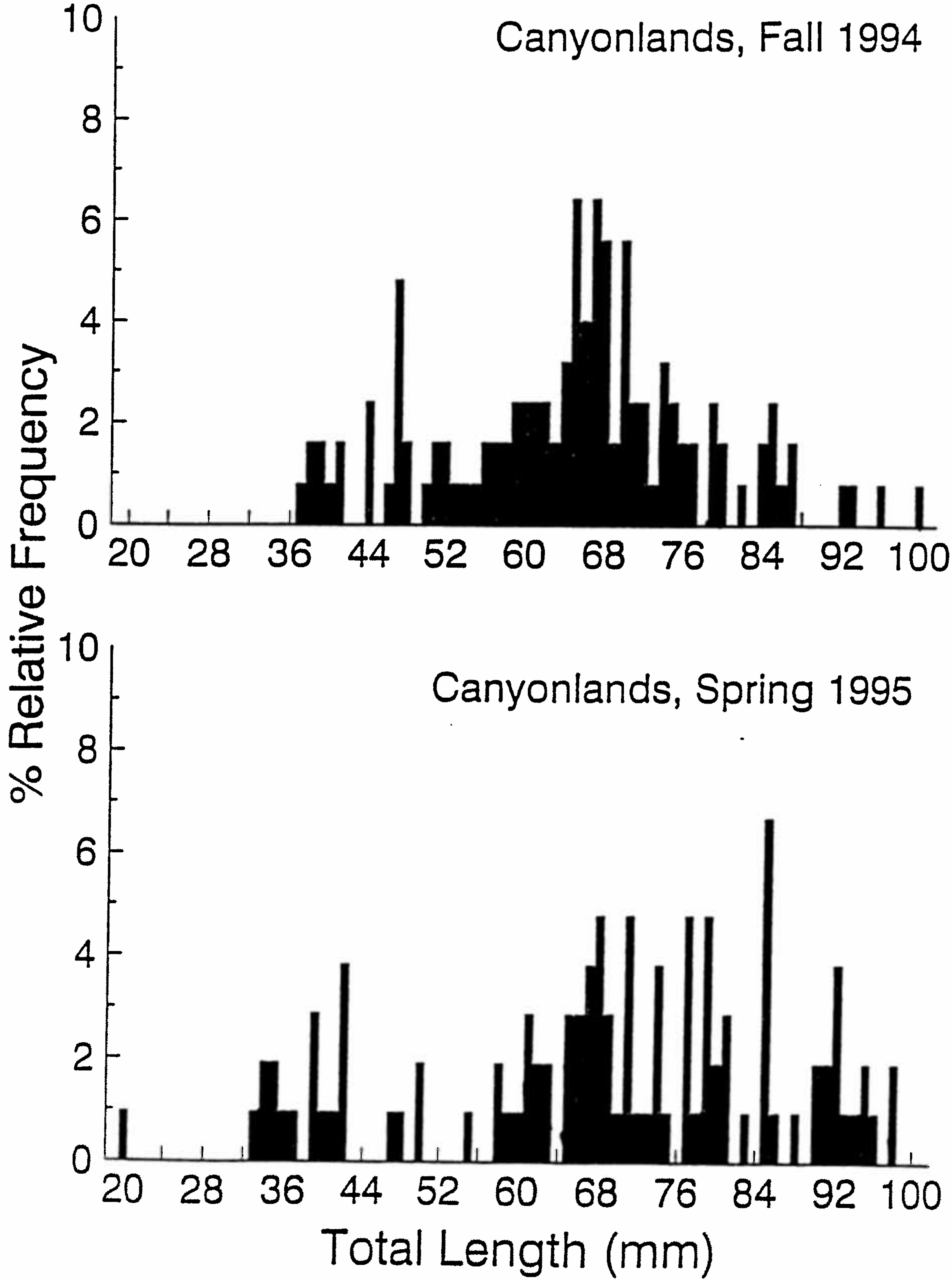

Figure 5. Length-frequency histograms for age-0 and age-1 Colorado squawfish in the Green River in Canyonlands National Park, Utah, autumn 1994 and spring 1995.

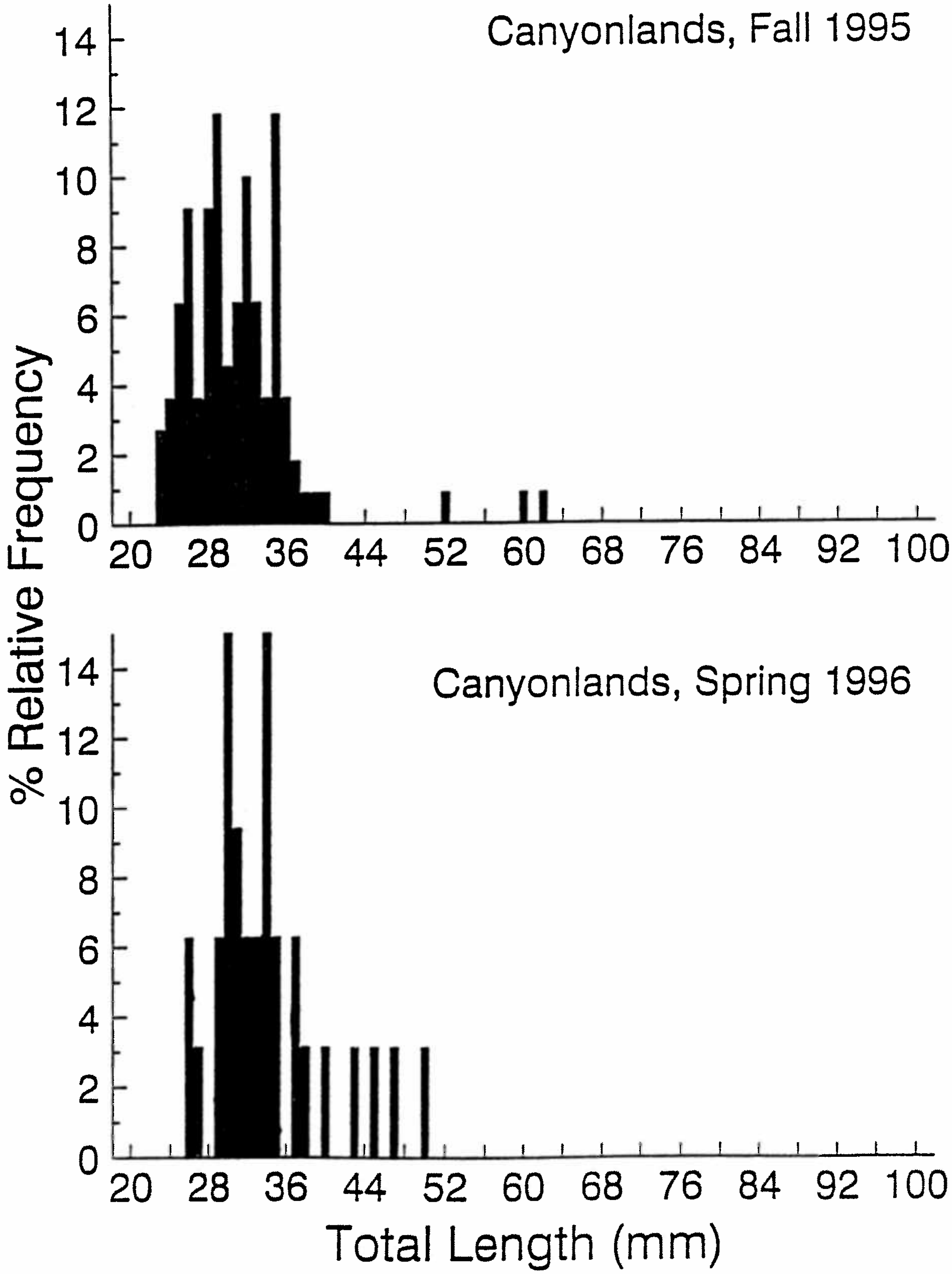

Figure 6. Length-frequency histograms for age-0 and age-1 Colorado squawfish in the Green River in Canyonlands National Park, Utah, autumn 1995 and spring 1996.

simulations confirmed that under thermal conditions in the Green River during summer 1994, larval Colorado squawfish could grow to 65 mm before we captured them in October. This value represents the size that would have been achieved by fish that were captured in drift nets on 28 June; fish captured as early as 20 June would have attained even larger size. Further evidence in support of rapid growth of Colorado squawfish during 1994 are results of the *Interagency Standardized Monitoring Program* (ISMP) which sampled age-0 Colorado squawfish in the Canyonlands reach several weeks before capture-recapture studies were conducted. The ISMP data also show that the distribution for Colorado squawfish total lengths was bimodal (Figure 7; McAda et al. 1995).

Population estimates. - Two characteristics of the capture data influenced our selection of an appropriate model for estimating population size of young Colorado squawfish. The first was that evidence of limited movement during autumn and spring sampling periods suggested that the assumption of geographical closure was not violated. The second was that previous observations suggested that probability of capture changed with water temperature and consequently may change on each sampling pass. To account for these characteristics, a model that assumed population closure but allowed probability of capture to vary on each sampling pass was selected (M_t or Darroch of Otis et al. 1978).

Data were sufficient to calculate population estimates for eight of ten occasions where capture-recapture sampling was conducted. Data were inadequate on two occasions when Colorado squawfish were scarce and no recaptures were observed. Both occasions were related to the same cohort (autumn 1994 and spring 1995) in the Jensen reach, where, despite good seining conditions, only 7 age-0 Colorado squawfish were captured in autumn and 28 in spring. Analysis of larval Colorado squawfish drift collected from the Yampa River for 1994 suggested that something disrupted emergence or drift of larval fish that summer (Bestgen et al. 1998). Less than 100 drifting larvae were captured that year, which is about an order of magnitude lower than typical catch. Thus, capture-recapture population estimates were not possible because few larvae migrated to nursery reaches during 1994.

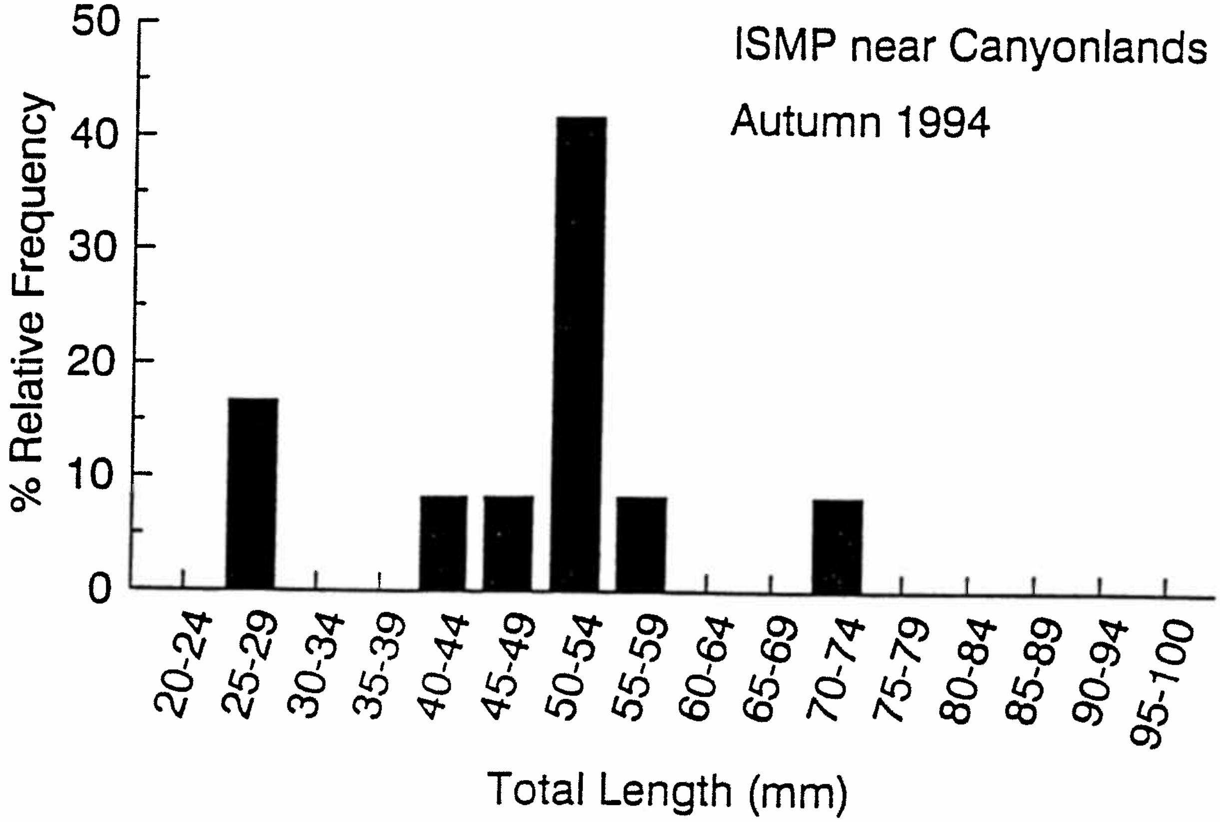

Figure 7. Length-frequency histogram for age-0 Colorado squawfish in the Green River near Canyonlands National Park, Utah, autumn 1994. Data collected by Interagency Standardized Monitoring Program.

Population estimates for the Canyonlands reach ranged from 3,722 age-0 fish (116 fish/km) in autumn 1994 to 140 age-1 fish (4 fish/km) in spring 1996 (Table 3). However, the highest densities were observed during the pilot year of this investigation in the Jensen reach: 230 fish/km in autumn 1992 and 129 fish/km in spring 1993. Coefficients of variation of estimates ranged from 0.13 to 0.60. Marking mortality was not accounted for in calculating the population estimates.

Table 3. - Population estimate (N), 95% confidence intervals (CI), standard error (SE), and probability of capture for each sampling pass p(j) for 1992 - 1996.

Occasion[a]	N	95% CI	SE	p(1)	p(2)	p(3)
Jensen Study Site						
autumn 92	3689	2836-4860	511.4	.08	.03	.04
spring 93	2129	1556-2994	349.4	.05	.04	.13
autumn 93	3679	2849- 4830	499.9	.12	.04	.04
spring 94	2297	1557- 3492	482.6	.05	.09	.03
autumn 94	no recaptures					
spring 95	no recaptures					
Canyonlands Study Site						
autumn 94	3793	3001-4864	471.2	.05	.09	.07
spring 95	2065	1530-2859	334.0	.08	.07	.06
autumn 95	2199	1623-3031	354.5	.06	.05	.04
spring 96	140	59- 443	83.9	.11	.07	.04

[a] Autumn 1992 and spring 1993 estimates are for 16-km reaches; all other estimates are for 32-km reaches.

Overwinter survival. - Survival probability estimates were computed for four of five winters included in this study. A survival estimate for the Jensen reach during winter 1994-1995 could not be calculated because population estimates for autumn and spring were not available. Estimates ranged from 0.06 to 0.62 (Table 4). Three estimates were similar and ranged from 0.56 to 0.62 with CVs ranging from 0.21 to 0.25. The fourth estimate was 0.06 (CV = 0.63) and was for the Canyonlands reach during winter 1995-1996.

Table 4. - Comparison of three methods for estimating overwinter survival. Estimates are means and their coefficient of variation (in parentheses).

Year	Mark-recapture	Combined CPUE[a]	Single pass CPUE[b]
Jensen Study Site			
1992-93	0.56 (0.22)	0.49 (0.43)	0.58 (0.52)
1993-94	0.62 (0.25)	0.38 (0.40)	0.56 (0.46)
1994-95	NA[c]	2.47 (0.59)	2.58 (1.18)
Canyonlands Study Site			
1994-95	0.56 (0.21)	0.39 (0.18)	0.35 (0.28)
1995-96	0.06 (0.63)	0.11 (0.56)	0.13 (0.47)

[a]Catch per unit effort (CPUE) estimate based on pooling three sampling passes through study site.
[b]CPUE estimate based on one sampling pass through study site.
[c]No recaptures.

A total of 1,645 fish were marked in autumn. Of these, 26 were recaptured the following spring. These recaptures were fewer than expected based on the number of fish marked in autumn, estimated capture probabilities, and overwinter survival probabilities. This pattern was consistent for all sampling occasions and sites. For the Jensen reach during spring 1993, expected catch of marked fish was 37, but only 5 were captured, and for spring 1994 expected catch was 62, but 5 were captured. For the Canyonlands reach during spring 1995 expected catch was 61, 16 were captured, and for spring 1996 expected catch was 3 fish but none were captured.

Comparison of CPUE and Capture-Recapture Estimates

There was a weak association between catch per seine haul and population-density estimates from capture-recapture methods ($r = 0.30$, $p = 0.47$; Figure 8). The weak correlation may have resulted from the two points derived from the Jensen reach during autumn 1992 and spring 1993, which associated relatively high population density with low CPUE, or from the

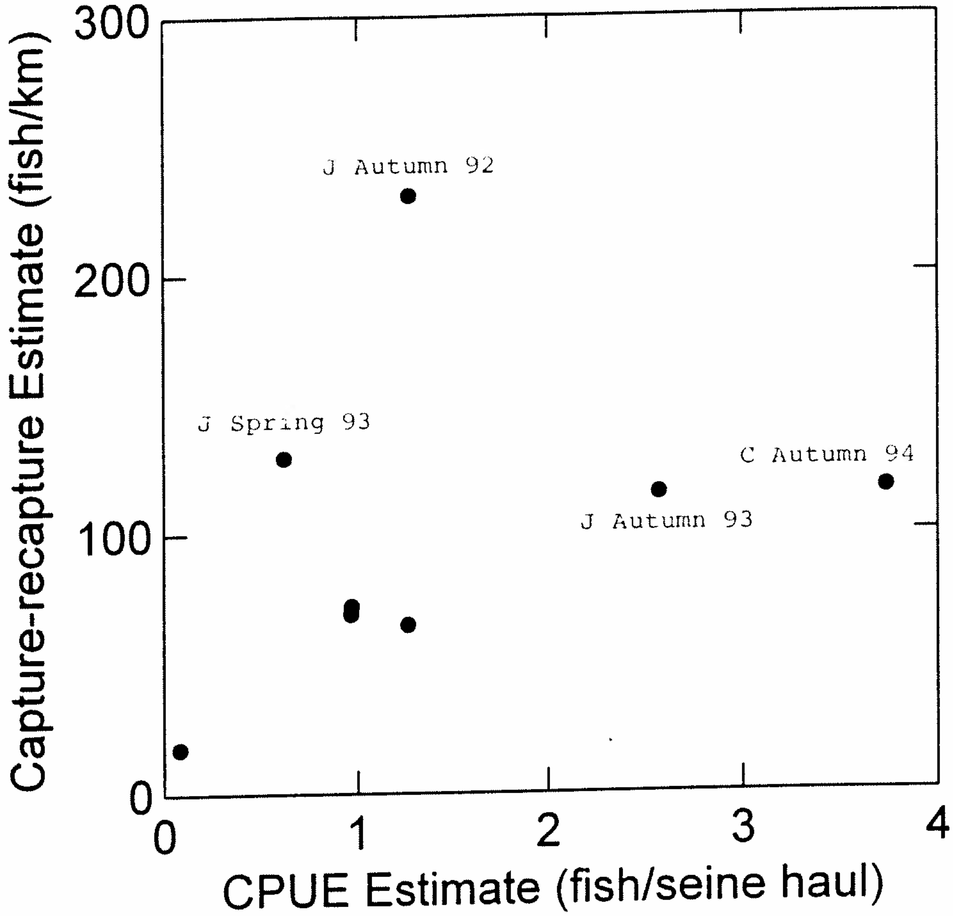

Figure 8. Relationship between abundance estimates from capture-recapture and catch per unit effort (CPUE) methods. Data are from Canyonlands (C) and Jensen (J) study sites on the Green River 1992-1996.

two points derived from the Jensen reach during autumn 1993 and Canyonlands reach during autumn 1994, which associated intermediate population density with high CPUE. In the first case, cool water temperatures may have driven young Colorado squawfish from backwaters and suppressed CPUE. Water temperatures on these occasions were cooler than those observed at any other time during this investigation: average main-channel temperatures were 9.0°C for autumn and 7.8°C for spring, whereas main-channel temperatures ranged from 11.3 to 15.0°C for all other sampling occasions. In the second case, warm water temperatures may have attracted young fish and contributed to high CPUE. Main channel temperatures averaged 12.0°C in the Jensen reach during autumn 1993, the warmest for that reach during the study; they averaged 15.0°C for the Canyonlands reach during autumn 1994, also the warmest during the study. The precision of the estimates that made up each of these points was relatively high, CV ranging from 0.13 to 0.37 for CPUE and from 0.13 to 0.17 for population density.

There was no significant difference between catchability coefficients in autumn and spring ($t = 1.24$, $df = 18$, $P = 0.23$). Mean (SD) catchability coefficients were 0.00066 (0.00034) for autumn and 0.00051 (0.00018) for spring. Similarity of catchability coefficients for autumn and spring may be a result of timing of sampling. Water temperatures were similar during autumn (range 8-16°C) and spring (range 6-16°C) sampling. Catchability coefficients were significantly correlated with main-channel temperature ($r = 0.66$, $P = 0.016$; Figure 9), but not with backwater temperature ($r = 0.54$, $P = 0.13$) or the difference between backwater and main channel temperature ($r = -0.14$, $P = 1.0$). The significant correlation between main-channel temperature and catchability coefficients suggests that regardless of their abundance, fewer fish are likely to be caught during relatively cool environmental conditions. This phenomenon represents a source of bias for CPUE estimates, but can be accounted for with an appropriate capture-recapture model.

Overwinter survival probabilities calculated based on CPUE estimates ranged from 61 to 217% of those from capture-recapture (Table 4). Catch-per-unit-effort estimates averaged 21% less than capture-recapture estimates that were relatively high (0.56 to 0.62). In contrast, when overwinter survival based on capture-recapture was low (0.06), the CPUE estimate was

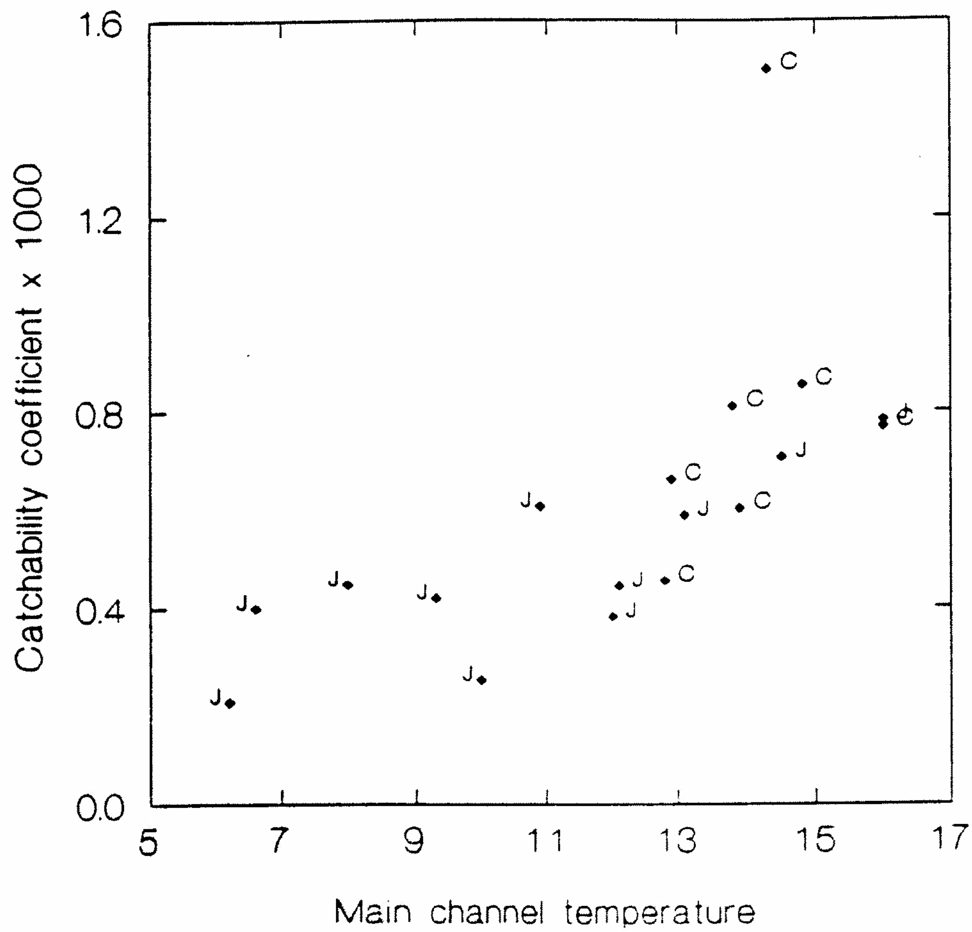

Figure 9. Relationship between main channel temperature and seining catchability coefficients for young Colorado squawfish captured from Canyonlands (C) and Jensen (J) study sites on the Green River 1992-1996.

100% higher. Capture-recapture (mean CV = 0.33) gave better precision than combined CPUE (mean CV = 0.43) or single pass CPUE (mean CV = 0.58).

Factors that Influence Overwinter Survival

Discharge. - There was no apparent relationship between overwinter survival and average daily discharge variability (Table 5; Figure 10). Inspection of the graphical plot showed that survival probability varied independently of coefficients of variation (CV) ranging from 0.135 to 0.174.

In contrast, there was evidence of a relationship between winter average daily discharge and survival. Overwinter survival was low in the Canyonlands reach when average daily discharge was 4005 cfs, but was relatively high at both study sites when discharge was $\leq$ 2555 cfs.

Size. - There was also evidence for dependence of overwinter survival on size of age-0 fish in autumn (Table 5; Figure 10). Survival was low for cohorts that had a mode TL $\leq$ 28 mm. No size-dependent survival effect was evident for cohorts with mode TL $\geq$ 39 mm. The form of the relationship for cohorts with mode TL ranging from 29 to 38 mm is uncertain because data are insufficient to describe it. The limited data suggest that a threshold model may provide a good approximation for the relationship and that the threshold is between 28 to 39 mm. It is likely that there is a significant amount of uncertainty associated with the value of the threshold in any given year because factors like timing of spring runoff, time of spawning, length of growing season, and severity of winter interact. Thus, the threshold for winter survival probably varies from year to year depending on combinations of these and other environmental factors.

Table 5. - Estimates of discharge- and size-related factors that may affect overwinter survival. Discharge estimates are for the Green River near Jensen or Green River, Utah, during the winter period from 1 October to 28 February.

Year	Mean Q[a] (cfs)	CV[b] Q	Mode Total Length (mm)	Survival Probability
Jensen Study Site				
1992-1993	1387	0.135	41	0.56
1993-1994	2521	0.174	39	0.62
1994-1995	1867	0.201	44	NA[c]
Canyonlands Study Site				
1994-1995	2555	0.170	67	0.56
1995-1996	4005	0.170	28	0.06

[a]Q = average daily discharge.
[b]CV = coefficient of variation.
[c]NA = no estimate for this occasion.

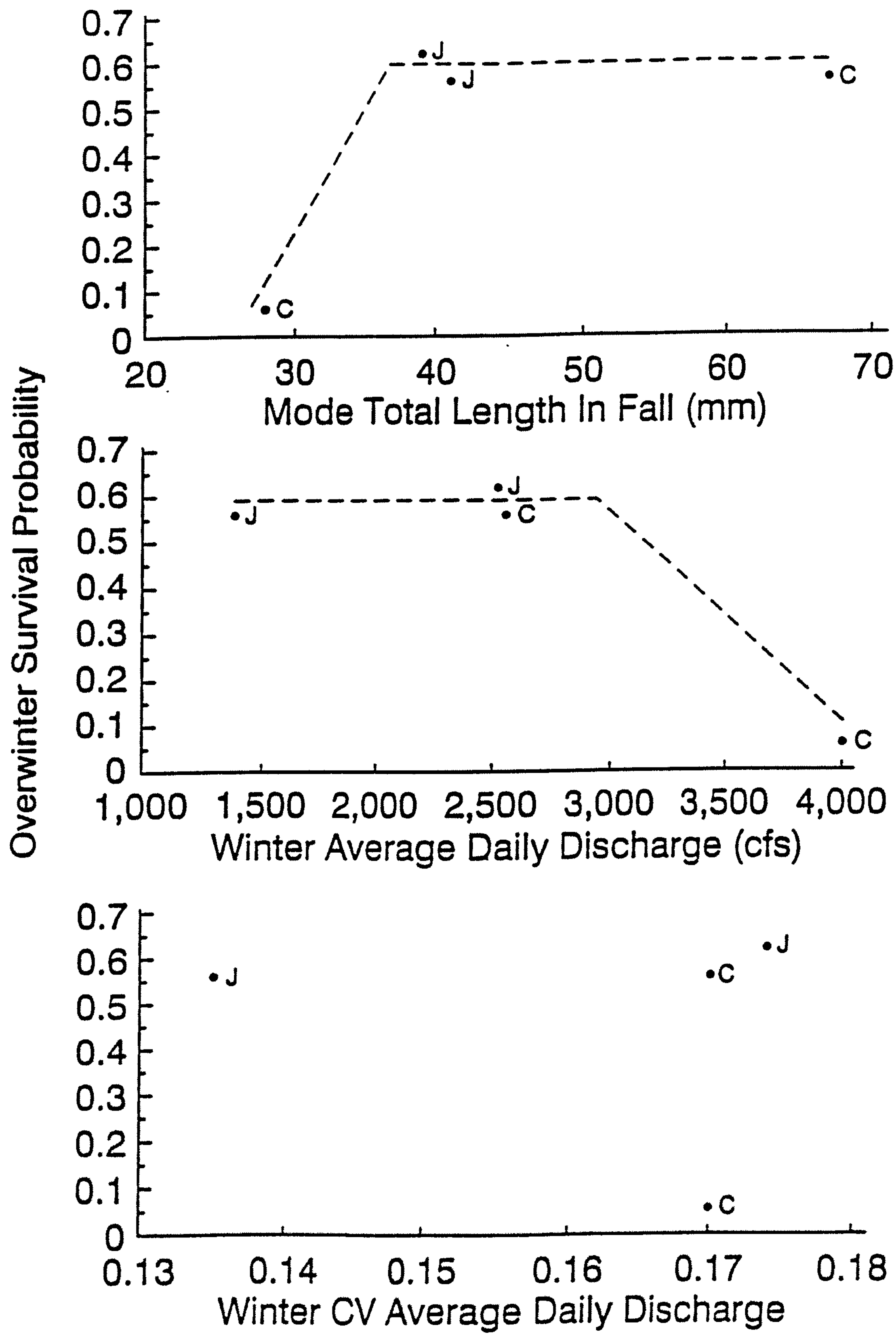

Figure 10. Relationships between overwinter survival probability and fish size in fall, average daily discharge, and coefficient-of-variation (CV) average daily discharge. Hypothetical relationships for survival as a function of total length in autumn and average daily discharge are illustrated by dashed lines. Data are from the Canyonlands (C) and Jensen (J) study sites (Table 5).

Discussion

Movement

During autumn and spring sampling, 99% of recaptured Colorado squawfish were in the 8- km section where they were originally marked. One fish (1%) moved downstream to an adjacent reach. These data suggest that young Colorado squawfish did not make long-distance movements during sampling periods; however, other data and observations suggest that they made local movements on a diel basis in response to environmental conditions. The relatively low probability of capture for each sampling pass suggests that only a small fraction (<5%) of the population of young Colorado squawfish within a reach were captured on each sampling occasion. Fish in backwaters can avoid capture by three mechanisms. First, they can avoid the seine. Second, they can occupy water too deep to seine. Only a small number of backwaters were too deep to seine and of these, the deep portion was less than 30% of total habitat. Third, fish can avoid capture by not being present in backwaters on a sampling occasion. We suspect that the small fraction of young Colorado squawfish captured on each occasion was in part due to movement in and out of backwaters in response to diel temperature fluctuations. General observations suggested that Colorado squawfish were more likely to be caught in backwaters in the afternoon when water temperatures were warm, compared to morning when water temperatures were cooler. This hypothesis is supported by results of the correlation analysis of catchability coefficients and water temperature. The analysis shows that Colorado squawfish were more likely to be caught when main-channel water temperature was warmer. Tyus (1991b) studied movements of young Colorado squawfish in the Green River during autumn and spring and presented similar results. He reported that abundance in backwaters varied on a diel basis that was positively related to backwater temperature and negatively related to temperature of the main channel. He also observed that young Colorado squawfish were capable of local movements between a variety of habitats including backwaters, eddies, and other shoreline habitats, and were able to cross the main channel without being transported downstream. Despite a high degree of local movement, some fish remained near the area where they were originally marked for at least one month (Tyus 1991b).

Seventy-three percent of age-0 Colorado squawfish that were marked in autumn and recaptured the following spring were in the same 8-km section where they were originally captured. These fish were captured in backwaters that were relatively large and deep. Twenty-seven percent of recaptured fish moved short distances downstream during winter and one fish moved 7.4-km upstream. Eight marked fish were found by other fishery investigators in the Canyonlands study site. All eight remained within the study site and some were at large for as long as 263 d.

The role of spring flooding in redistribution of age-1 Colorado squawfish remains unclear. Only one marked fish was captured during post-runoff surveys: it was 12-km downstream from where it was marked in spring. Four hypothetical processes can be offered to explain the scarcity of marked fish. First, they may have remained in their respective reaches, but moved to main-channel habitats that we did not seine. This process is consistent with what is known about Colorado squawfish life history. Habitat use of young Colorado squawfish changes as the fish grow (Holden 1977). Larger fish do not restrict their movements to backwaters and spend more time in deeper main-channel habitats. Second, they may have dispersed into flooded vegetation on islands and shorelines. This would have resulted in fish being more diffuse and difficult to sample during post-runoff surveys compared to low-discharge periods when they were concentrated in backwaters. Third, marked fish may have been redistributed by spring runoff to downstream reaches. This alternative would have had the effect of spreading marked fish over a broad area reducing the probability they would be recaptured. Other studies have demonstrated that flooding can displace or kill small fish (Harvey 1987; Minckley and Meffe 1987; Pearsons et al. 1992). If redistribution by flooding was extreme, marked fish might have been transported to river reaches that were beyond the areas encompassed by the post-runoff surveys. Finally, marked fish may have died, perhaps the result of predation or the physiological stress associated with the runoff period. It is unclear which of these processes were responsible for disappearance of marked fish after runoff. All four are consistent with what is known about young Colorado squawfish and their environment, and it is possible that they all contributed to the disappearance of marked fish.

Capture-Recapture Population Estimates

The Darroch population estimator that was used for analysis of capture data has several assumptions: (1) the populations were closed, (2) marks were retained for duration of the study, (3) marks were correctly interpreted and recorded, (4) capture probabilities varied on each sampling pass, and (5) capture and marking did not affect probability of capture (Otis et al. 1978). We believe these assumptions were met for the autumn and spring population estimates.

With regard to the first assumption, all capture-recapture studies were completed in less than 31 d and data show that fish moved only small distances during this time. Haines and Modde (1996) did a simulation study that explored affects of rates of immigration and emigration on capture-recapture population estimates. They concluded that population estimates would be biased by less than 5% if the closure assumption was violated by immigration or emigration at rates equal to those observed in the Green River.

Laboratory studies reported by Haines and Modde (1996) provide evidence that the second and third assumptions were not violated. They found that when the elastomer marking material was used on age-0 Colorado squawfish, 98% of the fish retained their marks for at least 21 d. Excellent retention increased the likelihood that marking patterns were correctly interpreted in the field. The elastomer marking material did not appear to be degraded by environmental conditions in fish marked in autumn and recaptured in spring. Marks retained their color and were easily recognized.

The assumption that marking did not affect probability of capture is the most likely assumption to be violated in our research. Haines and Modde (1996) monitored survival of marked fish held in laboratory conditions and reported that no post-marking mortality was observed after 21 d. In addition, they made extensive field observations on marked fish held overnight in enclosures and survival averaged 95%. In our study, survival of marked fish held overnight in enclosures in the field averaged 85%, but we attributed much of the mortality to the enclosures and weather conditions. If we discount survival trials with enclosure-induced mortality, marking survival was 95%. Uncontrolled marking mortality biases population estimates towards overestimates. The magnitude of bias can be quantified using the formula 1 -

mark survival rate; for example, if mark survival was 0.95, then our population estimates were overestimated by 5%.

Overwinter Survival

Estimating overwinter survival by dividing the spring population estimate by the autumn estimate assumes that the same population was sampled on each occasion. That is, there was no immigration or emigration of marked or unmarked fish during winter. Recaptures of fish in close proximity to where they were originally marked, and the scarcity of marked fish downstream of study reaches support this assumption. However, recaptures in spring of fish marked in autumn were fewer than expected. This result could have been due to (1) low overwinter mark retention, (2) reduced survival of marked fish compared to unmarked, or (3) emigration of marked fish from study reaches. We suspect that the third alternative, emigration during the winter period, is the most likely explanation. Reduced survival of marked fish probably contributed to this result, but does not account for a large percentage of the discrepancy between expected and observed capture of marked fish in spring. Occasional emigration of Colorado squawfish would be difficult to detect with the short-term monitoring used in our investigation. However, the cumulative change in abundance of marked fish over the 6-month period between autumn and spring would probably be detectable and may explain the difference between expected and observed capture of marked fish. This is one example of the importance of understanding movements of young Colorado squawfish. If more complete descriptions of immigration and emigration rates were available, it would be possible to use a capture-recapture model that explicitly considers movement of fish, thereby reducing potential bias so that the influence of other processes that influence overwinter survival could be studied.

Comparison of CPUE and Capture-Recapture Estimates

Our CPUE estimates were based on sampling entire backwater area and every backwater in a study reach. Our magnitude of effort was much higher than that employed in the ISMP. Consequently, our results are not directly comparable to the ISMP, but are useful for studying general properties of catch-effort methods.

We found a weak correlation between abundance estimates from capture-recapture and CPUE methods. This result suggests that CPUE does not provide reliable estimates of abundance. The cause of the weak correlation was attributed to reduced catch of Colorado squawfish in the Jensen reach during autumn 1992 and spring 1993, when abundance of fish was high, but water temperatures were relatively cold (main channel and backwater temperatures averaged 9.0 and 10.0°C in 1992 and 7.8 and 10.6°C in 1993). We showed that probability of capture per seine haul (catchability coefficient) declined with main-channel water temperature. During autumn 1992 and spring 1993, it is likely that cool water temperatures reduced efficiency of sampling for young Colorado squawfish. Capture-recapture analyses account for the reduced capture probabilities that result from variable environmental conditions, but CPUE methods do not.

Survival estimates calculated from CPUE data are based on the assumption that young Colorado squawfish were equally vulnerable to capture in autumn and the following spring. Evidence suggests that this assumption was not always met. For example, catchability coefficients for the Canyonlands reach during spring 1995 were about 50% less than the estimates for the previous autumn. Reduced catchability during spring caused the overwinter survival estimate from CPUE to be biased low (0.39) compared to the capture-recapture estimate (0.56). During the same year, Valdez and Cowdell (1996) used seine CPUE and estimated a survival probability of 0.37 for the lower nursery area. Valdez and Cowdell (1996) also reported that main channel temperatures were cooler during spring (12-14°C) compared to the previous autumn (16-24°C). This independent result supports our contention that cooler temperatures reduce seining efficiency and are a source of bias in CPUE survival estimates. In contrast, capture-recapture procedures account for the potential bias that may result from variable seining efficiency.

Survival estimates based on capture-recapture methods were more precise than those from CPUE. The average CV for capture-recapture was 0.33 compared to 0.43 for combined CPUE and 0.58 for single-pass CPUE. Single-pass CPUE estimates probably were most variable because different environmental conditions influenced seining efficiency on each sampling pass.

Advantages and Disadvantages of Capture Recapture and CPUE

Capture-recapture and CPUE methods both have strengths and weaknesses. Capture recapture is a more rigorous tool for estimating abundance of organisms, but this benefit has a cost. Capture-recapture methods require more effort: a three-person field crew required 6 d to complete three-pass sampling for a 32-km river reach. As a consequence, capture-recapture methods are difficult to employ for long river reaches, but for limited reaches, they provide increased precision with only moderately greater expenditure of resources. Capture-recapture methods also have assumptions that must be considered. Of these, the assumption that capture and marking does not affect probability of capture is the most likely to be violated. This assumption implies that marking does not affect survival of young Colorado squawfish. Our studies showed that on average, survival was reduced by marking even when great care was taken to alleviate handling stress. The consequence of this result is that sampling and marking procedures for small Colorado squawfish must be conducted by experienced field crews that are familiar with procedures for reducing physiological stress and can be relied upon to employ them. Use of inexperienced crews will probably result in higher mortality rates of marked fish and consequently, biased population estimates.

An advantage of capture-recapture population estimates is that they are not biased by environmental fluctuations (e.g., water temperature) that may affect capture probability. It is widely recognized that accurate population estimation requires use of models that account for variable capture probabilities (White et al. 1982:7). A second advantage of capture-recapture methods is that the same data can be used to calculate CPUE estimates of abundance. Thus, capture-recapture data can be collected without sacrificing the ability to make comparisons with historical records. A third advantage is that capture-recapture estimates have greater precision than CPUE. This is probably due to its ability to account for variable capture probabilities.

The usefulness of CPUE estimates can only be realized when long-term data are available or when long river reaches must be monitored. Study of long-term data collected by CPUE may permit description of trends, but the value of interpreting abundance estimates that are of uncertain precision is questionable. Catch-per-unit-effort methods that are currently employed by researchers in the Colorado River basin require less time and resources compared to capture-recapture. Field crews employing CPUE methods can move relatively quickly and routinely cover 193-km reaches in the Green River in four days. Unlike capture-recapture, CPUE estimates are not influenced by mortality from handling stress on captured fish, though mortality may occur.

The main disadvantage of CPUE methods is that they do not account for variable capture probabilities that may be caused by environmental conditions. For example, cool water temperatures may alter fish behavior, making them less vulnerable to capture. As another example, flow alterations may increase the amount of backwater habitat available, dispersing the fish and making them less vulnerable to capture. As a consequence, the accuracy and precision of abundance estimates obtained with these methods are unknown.

Relationship Between Survival, Energy Reserves, and Discharge

Winter survival of small fish is related to their ability to accumulate energy reserves (Oliver et al. 1979; Shuter and Post 1990). Small fish are at a disadvantage because basal metabolism increases as size decreases, but there is no corresponding increase in energy storage capacity. Mortality of young Colorado squawfish during winter has been attributed to exhaustion of lipid reserves (Thompson et al. 1991). Physical damage from anchor and frazil ice has also been suggested as a source of mortality (Valdez 1995). Valdez and Masslich (1989) reported that daily flow fluctuations during winter increased movement of adult Colorado squawfish. It is likely that discharge fluctuations affect young Colorado squawfish in a similar manner. Our field observations showed that when slight increases in discharge inundated backwaters they became flow-through habitats and were abandoned by young Colorado squawfish.

It is hypothesized that nursery habitats provide favorable conditions for survival of young Colorado squawfish including: refugia from current, access to preferred thermal conditions, and a productive environment where prey are likely to be encountered. When discharge fluctuations inundate nursery habitats and transform them into flowing environments these survival advantages are eliminated. Resident fish are flushed into the surrounding system and incur increased risk of injury, predation, and metabolic costs associated with the search for another nursery habitat.

Water temperature is a major controlling factor on the physiology of fish and therefore on their swimming ability (Beamish 1978). At water temperatures below optimum, sustained and prolonged swimming speeds of fish decline as water temperature declines. Scope for activity also declines at temperatures below optimum. Thus, during winter, Colorado squawfish swim slower and must expend a greater percentage of their available energy to move a given distance. The implication of these characteristics is that redistribution of young Colorado squawfish as a result of nursery habitat inundation is potentially more important in winter than in summer because it is energetically more costly.

To evaluate the potential influence of energy reserves or discharge on overwinter survival of age-0 Colorado squawfish we studied three factors: winter discharge variability, winter discharge magnitude, and fish size in autumn. We found no evidence that overwinter survival was related to average daily discharge variability. It is important to note that the measure of discharge variability that we used does not reflect diel fluctuations that result from electric power generation at Flaming Gorge Dam. The CV for discharge does reflect daily variation within the winter period. We did find evidence that survival was related to discharge magnitude and fish size. Because of the limited scope and duration of this study, only four data points were available for this analysis. Trends in this limited data set should be used to develop hypotheses about causal mechanisms that influence survival of young Colorado squawfish.

Conclusions

We found little evidence that abundance estimates from CPUE accurately reflect the number of young Colorado squawfish in study reaches in the Green River. There was only a weak correlation ($r = 0.50$, $P = 0.14$) between estimates of abundance from CPUE and mark-recapture. On several occasions, CPUE estimates had precision that was comparable to that achieved with mark-recapture, but the estimates differed by as much as 217%. Inaccuracy and greater variability of CPUE was attributed to effects of water temperature on capture probability. Evidence suggests that young Colorado squawfish are less likely to be caught when water temperatures are cool, regardless of their abundance.

Overwinter survival probabilities of age-0 fish ranged from 0.06 to 0.62. Three of four estimates were similar and ranged from 0.56 to 0.62. Low overwinter survival (0.06) during 1995-1996 may have been due to small size of age-0 fish in autumn or relatively high winter discharge.

Recaptures of marked age-0 and age-1 Colorado squawfish showed that they moved less than 16 km downstream during sampling periods that ranged from 2 to 21 days. Similarly, age-0 fish that were marked in autumn and recaptured the following spring moved less than 16 km downstream after being at large for 170 to 200 days.

By integrating results of this research with larval-drift studies, larval-growth studies, water-discharge data, and water-temperature data, a synthetic account can be constructed of how age-0 and age-1 Colorado squawfish responded to environmental conditions in a given year. The limited data generated by this research are insufficient to predict the affects of environmental conditions on early life-stage cohorts, but do suggest that continued study may link characteristics like size, abundance, and overwinter survival probability to environmental conditions that strongly influence them.

Recommendations

1. Conduct capture-recapture population estimates of age-0 Colorado squawfish on a regular basis in historically productive areas, or in areas of special concern within the upper Colorado River basin. These data can be used as a quality-assurance check to evaluate performance of other population monitoring tools that may be strongly influenced by environmental conditions.

2. Conduct studies that describe local and long-term movement of young Colorado squawfish during winter (October to March). This information will expand our understanding of potential effects of winter discharge fluctuations on Colorado squawfish.

3. Abundance estimates for age-0 Colorado squawfish should be made in autumn and the following spring. Evidence suggests that significant mortality may occur during winter. By generating estimates in autumn and spring, factors that influence abundance of age-0 fish during their first summer can be separated from factors that affect overwinter survival.

References

Beamish, F. W. H. 1978. Swimming Capacity. Pages 101-189 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, volume 7. Academic Press, New York.

Bestgen, K. R. 1996. Growth, survival, and starvation resistance of Colorado squawfish larvae. Environmental Biology of Fishes 46:197-209.

Bestgen, K. R., D. W. Beyers, G. B. Haines, and J. A. Rice. 1997. Recruitment models for Colorado squawfish: Tools for evaluating relative importance of natural and managed processes. Final report to National Park Service, Cooperative Parks Study Unit, Fort Collins, Colorado, and Midcontinent Ecological Science Center, U. S. Geological Survey, Fort Collins, Colorado.

Bestgen, K.R., R.T. Muth, and M.A. Trammell. 1998. Downstream transport of Colorado squawfish larvae in the Green River drainage: temporal and spatial variation in abundance and relationships with juvenile recruitment. Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River Basin, U. S. Fish and Wildlife Service, Denver, Colorado.

Carlson, C. A., and R. T. Muth. 1989. The Colorado River: lifeline of the American Southwest. Pages 220-239 *in* D. P. Dodge, editor. Proceedings of the International Large River Symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106, Ottawa.

Crist, L., and R. D. Williams. 1994. Five year Flaming Gorge research program, FY 1995. Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River Basin, U. S. Fish and Wildlife Service, Denver, Colorado.

Haines, G. B., and T. Modde. 1996. Evaluation of marking techniques to estimate population size and first-year survival of Colorado squawfish. North American Journal of Fisheries Management 16:905-912.

Haines, G. B., and H. M. Tyus. 1990. Fish associations and environmental variables in age-0 Colorado squawfish habitats, Green River, Utah. Journal of Freshwater Ecology 5:427-435.

Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. Transactions of the American Fisheries Society 116:851-855.

Holden, P. B. 1977. Habitat requirements of juvenile Colorado River squawfish. U.S. Fish and Wildlife Service, Report FWS/OBS-77/65, Fort Collins, Colorado.

McAda, C. W., J. W. Bates, J. S. Cranney, T. E. Chart, W. R. Elmblad, and T. P. Nesler. 1994. Interagency standardized monitoring program: summary of results, 1986-1992. Final Report. Recovery Implementation Program for the Endangered Fishes of the Upper Colorado River Basin, U.S. Fish and Wildlife Service, Denver, Colorado. 73 pp. + appendices.

McAda, C. W., W. R. Elmblad, T. E. Chart, K. S. Day, M. A. Trammell. 1995. Interagency standardized monitoring program: summary of results, 1994. Annual Report. Recovery Implementation Program for the Endangered Fishes of the Upper Colorado River Basin, U.S. Fish and Wildlife Service, Denver, Colorado. 17 pp. + appendices.

Minckley, W. L., and G. K. Meffe. 1987. Differential selection by flooding in stream fish communities of the arid American Southwest. Pages 93-104 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Nesler, T. P., R. T. Muth, and A. F. Wasowicz. 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. American Fisheries Society Symposium 5:68-79.

Oliver, J. D., G. F. Holeton, and D. E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Transactions of the American Fisheries Society 108:130-136.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs No. 62.

Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. Transactions of the American Fisheries Society 121:427-436.

Prentice, E.F., T.A. Flagg, and C.S. McCutcheon. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Pages 317-322 in N.C. Parker and five co-editors. Fish marking techniques. American Fisheries Society Symposium 7, Bethesda, Maryland.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin 191, Journal of the Fisheries Research Board of Canada.

Robson, D. S. and G. R. Spangler. 1978. Estimation of population abundance and survival. in S.D. Gerking ed. Ecology of freshwater water fish production. John Wiley and Sons, New York.

Seber, G. A. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, New York, USA.

Shuter, B. J. and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119:314-336.

Thompson, J. M., E. P. Bergersen, C. A. Carlson, and L. R. Kaeding. 1991. Role of size, condition, and lipid content in the overwinter survival of age-0 Colorado squawfish. Transactions of the American Fisheries Society 120:346-353.

Tyus, H. M. 1985. Homing behavior noted for Colorado squawfish. Copeia 1985:213-215.

Tyus, H. M. 1990. Potamodromy and reproduction of Colorado squawfish in the Green River Basin, Colorado and Utah. Transactions of the American Fisheries Society 119:1035-1047.

Tyus, H. M. 1991a. Ecology and management of Colorado squawfish. Pages 370-402 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction: native fish management in the American Southwest. University of Arizona Press, Tucson.

Tyus, H. M. 1991b. Movements and habitat use of young Colorado squawfish, Ptychocheilus lucius, in the Green River, Utah. Journal of Freshwater Ecology 6(1):43-51.

Tyus, H. M., and G. B. Haines. 1991. Distribution, habitat use, and growth of age-0 Colorado squawfish in the Green River basin, Colorado and Utah. Transactions of the American Fisheries Society 120:79-89.

U. S. Fish and Wildlife Service. 1992. Biological opinion on the operation of Flaming Gorge Dam. U. S. Fish and Wildlife Service, Denver, CO.

Valdez, R. A. 1995. Synthesis of winter investigations of endangered fish in the Green River below Flaming Gorge Dam. Five Year Flaming Gorge Research Program - FY 94, Study No. 18-11. Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River Basin. U.S. Fish and Wildlife Service, Denver, Colorado.

Valdez, R. A., and B. Cowdell. 1996. Survival of age-0 Colorado squawfish in the Green River. Interim Report-1996. Prepared for Utah Division of Wildlife Resources, Salt Lake City, Utah, Contract No. 90-2558, by BIO/WEST, Inc.

Valdez, R. A., and W. J. Masslich. 1989. Winter habitat study of endangered fish - Green River. Wintertime movement and habitat of adult Colorado squawfish and razorback suckers. BIO/WEST Report No. 136-2 185 pp.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Los Alamos, New Mexico.

Wilkinson, L. 1990. SYSTAT: the system for statistics. Evanston, Illinois. SYSTAT, Inc.

Wydoski, R. S., and J. Hamill. 1991. Evolution of a cooperative recovery program for endangered fishes in the Upper Colorado River Basin. Pages 123-140 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction. University of Arizona Press, Tucson.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

Appendix 1a. Capture-recapture data for autumn 1992 and spring 1993, Green River between river km 467-483. j = sample occasion, M(j) = number of marked fish prior to sample, m(j) = number of marked fish caught, u(j) = number of unmarked fish caught, N = number of backwaters or low velocity channel sites sampled, MC = average main channel temperature, BA = average backwater temperature.

j	M(j)	m(j)	u(j)	Dates	N	MC (C°)	BA (C°)
				Autumn 92			
1	0	0	383	09/22-10/13	9	12.5	14.0
2	297	5	115	10/13-10/14	18	10.0	11.0
3	297	7	150	10/21-10/22	24	8.0	9.0
				Spring 93			
1	0	0	104	04/06-04/08	16	6.6	9.2
2	104	14	79	04/12-04/15	17	6.2	9.9
3	183	14	247	04/19-04/22	29	10.9	12.6

Appendix 1b. Capture-recapture data for autumn 93 and spring 94, Green River between river km 451-483. j = sample occasion, M(j) = number of marked fish prior to sample, m(j) = number of marked fish caught, u(j) = number of unmarked fish caught, N = number of backwaters or low velocity channel sites sampled.

j	M(j)	m(j)	u(j)	Dates	N	MC	BA
				Autumn 93			
1	0	0	516	09/27-10/05	33	14.5	17.5
2	454	19	139	10/12-10/13	21	12.1	13.1
3	593	25	128	10/15-10/21	16	9.3	10.5
				Spring 94			
0	0	0	0	03/31-04/01	10		
1	0	0	108	04/12-04/14	27	12.0	15.2
2	108	12	184	04/18-04/21	26	16.0	18.7
3	285	3	58	05/02-05/04	16	13.1	19.9

Appendix 1c. Capture-recapture data for autumn 1994 and spring 1995, Green River between river km 451-483. j = sample occasion, M(j) = number of marked fish prior to sample, m(j) = number of marked fish caught, u(j) = number of unmarked fish caught, N = number of backwaters or low velocity channel sites sampled.

j	M(j)	m(j)	u(j)	Dates	N	MC	BA
				Autumn 94			
1	0	0	3	10/09-10/10	21	13.0	12.0
2	3	0	3	10/11-10/12	15	12.6	14.8
3	6	0	1	10/13-10/14	12	13.7	14.7
				Spring 95			
1	0	0	5	04/18-04/24	22	11.0	14.2
2	5	0	23	04/25-04/26	23	13.1	17.1
3	28	0	0	04/27-04/28	22	11.5	13.0

Appendix 1d. Capture-recapture data for autumn 1994 and spring 1995, Green River between river km 43-76. j = sample occasion, M(j) = number of marked fish prior to sample, m(j) = number of marked fish caught, u(j) = number of unmarked fish caught, N = number of backwaters or low velocity channel sites sampled.

j	M(j)	m(j)	u(j)	Dates	N	MC	BA
				Autumn 94			
1	0	0	198	10/04-10/05	17	16.0	16.6
2	198	8	323	10/06-10/07	21	14.3	15.5
3	520	45	221	10/08-10/09	27	14.8	16.3
				Spring 95			
1	0	0	169	03/24-03/25	34	12.9	14.6
2	169	16	134	03/25-03/27	45	N.A.[a]	
3	303	15	112	03/27-03/28	43	N.A.[a]	

[a] no data.

1. For autumn, of the 45 recaps on 3rd pass, 34 from 2nd pass, 10 from 1st pass, 1 from both 2nd and 3rd pass.
2. During autumn, one mortality from 2nd pass.
3. For spring, of the 31 recaps on 3rd pass, 18 from 2nd pass, 13 from 1st pass, 0 from both 2nd and 3rd pass.
4. During the spring, 16 recaps from fish marked previous autumn.

Appendix 1e. Capture-recapture data for autumn 1995 and spring 1996, Green River between river km 43-76. j = sample occasion, M(j) = number of marked fish prior to sample, m(j) = number of marked fish caught, u(j) = number of unmarked fish caught, N = number of backwaters or low velocity channel sites sampled.

j	M(j)	m(j)	u(j)	Dates	N	MC	BA
				Autumn 95			
1	0	0	147	10/10-10/12	38	13.8	16.9
2	138	2	100	10/12-10/14	46	13.9	14.9
3	238	1	97	10/14-10/15	52	12.8	15.3
				Spring 96			
1	0	0	18	04/19-04/20	37	10.9	13.1
2	15	0	10	04/21-04/22	40	11.1	12.9
3	25	2	4	04/23-04/24	39	11.8	14.2

1. Autumn, 9 mortalities on the 1st pass.
2. Autumn, the recap on the 3rd pass was marked on the 1st pass.
3. Spring, 3 mortalities on the 1st pass.
4. Spring, of the 2 recaps on 3rd pass, 1 was marked on 1st pass and one on the 2nd pass.