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Status and Trends of the Endangered Colorado Squawfish in the Upper Colorado River

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Abstract.—Status of the Colorado River population of the endangered Colorado squawfish *Ptychocheilus lucius* (recently renamed the Colorado pikeminnow) was investigated by (1) estimating adult numbers, (2) evaluating frequency of reproduction and recruitment, (3) identifying trends via changes in size structure over time, and (4) examining historical accounts for clues to former abundance. Adults and subadults were systematically captured from 278 km of river during 1991–1994. Larvae and age-0 fish were systematically sampled in two reaches during 1986–1994. Estimated number of adults in the upper 98 km averaged 253 individuals; estimated annual adult survival rate was 0.86. In the lower 181 km, estimates of subadults and adults combined averaged 344 individuals. A sizable pulse of subadults 300–400 mm long found in the lower reach in 1991 were from three year-classes, 1985–1987. By 1992, these were distributed throughout the river. Although catch rates of larger adults did not increase significantly in the upper reach during 1991–1994, catch rates of fish less than 550 mm long increased fivefold. Size-frequency analysis of lower-reach fish indicated the 1985–1987 cohorts were the largest produced since before 1977, and no similarly strong year-classes were produced subsequently. Estimated years of origin of these recruiting fish coincided with years of higher-than-average catch rates of larvae and age-0 fish in the upper reach and catch rates in subsequent years there were comparatively low. Very few individuals less than 450 mm long were found in the upper reach during the past 15 years, suggesting that recruitment there is from colonization from the lower reach. In contrast, significant numbers of fish less than 400 mm in total length occurred in the upper reach during the mid-1970s. Abundance appears much lower than suggested in historical accounts. Low adult numbers and sporadic pulses of recruitment may make this population vulnerable to extirpation. Though adult survival rate is probably fairly constant, recruitment is highly variable and may represent the most important demographic factor to population persistence.

Introduction

Colorado squawfish *Ptychocheilus lucius* (recently renamed Colorado pikeminnow; Nelson et al. 1998) were historically distributed throughout warmwater reaches of the Colorado River basin from Wyoming, Utah, and Colorado south to the Gulf of California (Miller 1961). By the 1970s they were extirpated from the Colorado River basin below Glen Canyon Dam (entire lower basin) and from sections of the upper basin as a result of major alterations to the riverine environment (Moyle 1976). Having lost some 80% of its former range, the Colorado squawfish was federally listed as an endangered species in 1967 (U.S. Office of the Federal Register 32:43[1967]:4001).

Colorado squawfish are presently restricted to the upper Colorado River basin and inhabit warmwater reaches of the Colorado, Green, and San Juan rivers and associated tributaries. The Green River and its two large tributaries (White and Yampa rivers) support the largest (Tyus 1991) and perhaps most viable (Gilpin 1993) population, whereas the San Juan River contains the smallest population (Platania et al. 1991). A third population persists in the upper Colorado River, but relatively low catch rates of adults and young (Valdez et al. 1982; Osmundson and Kaeding 1989; McAda et al. 1994) suggest this population may have limited viability. Because of the endangered status of this fish, assessing persistence potential of these smaller populations is important in assessing overall species viability.

We investigated the status of the upper Colorado River population by assessing current demographics and relating this to past and future demographic trends. Analyses included (1) estimating the size of the adult population, (2) determining the extent or frequency of reproduction and recruitment, (3)

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identifying demographic trends via temporal changes in age or size structure, and (4) examining historical accounts to reveal clues to former abundance. Systematic, riverwide sampling and marking of adult and subadult Colorado squawfish was conducted during a 4-year period to address analyses 1–3. In addition, we evaluated age-0 abundance, monitored during a 9-year period, and size-frequency data, collected by other researchers over 20 years. We then discuss the potential for population persistence based on these analyses and the present trends in habitat alteration.

Methods

Study area.—The study area included the entire portion of the Colorado River occupied by Colorado squawfish upstream of the Green River confluence and the lower 3.5 km of the Gunnison River upstream to the base of the Redlands diversion dam. Colorado River locations are described in river kilometers (rkm) converted from river miles as mapped by Belknap and Belknap (1974). The study area extended from the Green River confluence (rkm 0.0) upstream to rkm 298.1 at Palisade, Colorado, where further upstream movement of fish is blocked by two diversion dams.

Based on the distribution pattern of adults and juveniles, we partitioned the study area into two major reaches, upper and lower (described in Osmundson et al. 1998, this issue), and excluded from study the intervening 19-km Westwater Canyon. To examine distribution of adults within the upper reach, three subreaches were identified based on discharge, average gradient, and landform type. The upper subreach (rkm 298.1–275.1), in an alluvial valley, had mean discharge of 110 m^3/s and average gradient of 1.70 m/km. The middle subreach (rkm 275.1–245.5), in the same alluvial valley, had mean discharge of 175 m^3/s and average gradient of 1.27 m/km. The lower subreach (rkm 245.5–200.0), largely canyon bound, had mean discharge of 175 m^3/s and average gradient of 0.91 m/km. These lower, middle, and upper subreaches correspond to strata 5, 6, and 7, respectively, described in Osmundson et al. (1998).

Subadult and adult capture efforts.—Subadult (250–500 mm long) and adult (450–900 mm long) Colorado squawfish were captured from late April to mid-June 1991–1994 in backwaters throughout the entire study area. Subadults and adults congregate in these low-velocity habitats during spring runoff when main-channel flows increase dramatically (Osmundson and Kaeding 1989). Fish were actively entrapped in nets by a method we dubbed ‘‘scare and snare.’’ Using a 4.3-m-long johnboat, we first blocked the open end of each backwater with a trammel net; the boat then entered the backwater by passing over the net with the motor raised. To scare fish toward the net, the boat was vigorously motored back and forth beginning at the far end of the backwater and working toward the mouth. Nets were pulled as soon as sufficient ‘‘scare’’ effort was expended (5–15 min, depending on backwater size). In very large backwaters or flooded ponds, additional nets were set once the mouth was blocked. Trammel nets were 1.8 m deep with a 2.5-cm-bar-mesh inner panel and a 25-cm-bar-mesh outer wall. These nets captured Colorado squawfish as small as 259 mm (all fish lengths reported as total length) but caused gill damage in some small individuals. After the first year, finer-mesh netting (1.3-cm-bar inner mesh and 18-cm-bar-mesh outer wall) was used in the lower reach to prevent gill damage.

Ensnared Colorado squawfish were placed in a live well until all fish were removed from the nets. Fish were anesthetized, measured for maximum total length (Anderson and Gutreuter 1983), and electronically scanned for the presence of a passive integrated transponder (PIT) tag (Biomark, Inc., Boise, Idaho). If a PIT tag was not found, one was implanted in the body cavity by using a hypodermic needle inserted 2–5 mm posterior to the base of the left pelvic fin. Fish were released after recovery from the anesthetic.

Three passes through the upper study reach were made each spring, and every backwater that might hold Colorado squawfish was netted in each pass. Each pass generally took 7–9 d to complete. In the lower reach, two passes were made each spring (except in 1991 when only one pass was made). In some portions of both reaches where backwater habitats were rare, both shorelines were electrofished with a 4.9-m-long johnboat equipped with a Coffelt VVP-15 electrofisher (Coffelt Manufacturing, Flagstaff, Arizona) that produced pulsed DC. Capture data for portions of some passes were also supplemented with fish electrofished by the Colorado Division of Wildlife (lower subreach of the upper study reach) and U.S. Fish and Wildlife Service (lower 3.5 km of Gunnison River).

Survival rate.—Capture–recapture data from the multiple passes were used for estimating survival rates in the upper and lower reaches by using Cormack–Jolly–Seber (CJS) models (see Lebreton et al. 1992) because no assumptions were needed concerning abundance, recruitment, or trends in population abundance. Because comprehensive literature exists on CJS models, data analysis based on these models, and analysis strategy including model selection (e.g., Buckland 1980; Pollock 1982; Burnham et al. 1987; Pollock et al. 1990; Burnham and Anderson 1992; Lebreton et al. 1992; Anderson et al. 1994; Burnham et al. 1995), only minimal information is provided here.

The analysis strategy was to use the program RELEASE (Burnham et al. 1987) to compute the goodness of fit of the general time-specific CJS model for the capture data. With an acceptable fit, program SURGE (Lebreton et al. 1992) was used to find the best model out of a set of models considered. Akaike's Information Criterion (AIC) was used for model selection (Akaike 1973; Burnham and Anderson 1992; Lebreton et al. 1992; Anderson et al. 1994; Burnham et al. 1995). The AIC is a relative measure of how appropriate a model is for a given set of data, with the ''best'' model having the smallest AIC (AIC_{min}). The difference in AIC value between a given model and the best model is defined as ΔAIC. Models within about $\Delta AIC = 2$ of the best model were considered plausible alternative models for the data.

The CJS model is based on two types of parameters: survival rate (ϕ) and capture probability (p), the probability of an individual being caught (see Lebreton et al. 1992), which may vary by capture occasion and time interval between occasions. A circumflex (ˆ) over a parameter indicates it is estimated (e.g., $\hat{p}$). Models considered were the fully time-specific CJS model and simpler models based on a mixture of features: constant per-unit time survival rates, year-specific survival rates, season-specific survival rates, and capture rates that could be year- or season-specific or constant, or that could show a linear trend on either occasion or year. Models with full time variation parameters were denoted by $\{\phi_t, p_t\}$ and with no time variation by $\{\phi, p\}$. Intermediate models included $\{\phi_t, p\}$ and $\{\phi, p_t\}$. The notation p_{year} was used to denote different capture rates between years with constant capture rates for the three within-year capture occasions. Survival rates differing in the intervals between sampling (three intervals for the upper reach) were denoted by $\phi_{seasons}$. Models with similar survival rates in short intervals (t = 3 weeks or roughly 0.06 year) between spring samples but different rates in the time interval over the rest of the year (t = roughly 0.88 year in the upper reach) were denoted $\phi_{short;\ long}$. A model was also considered where no mortality was assumed during the short time intervals, and the survival parameter was denoted $\phi_{short\ =\ 1;\ long}$.

The CJS models were also used to ascertain evidence of time trends in capture rates, which would affect the interpretation of time trends in abundance. These analyses were based on fitting CJS models with capture probabilities (p_i) having a linear trend over time. Denoted p_T, these models used logit $(p_i) = \log_e [p_i/(1 - p_i)]$ (see e.g., Burnham et al. 1996; Franklin et al. 1996). A plausible alternative model sets capture probabilities equal within a year, but with a trend over the four years (denoted p_Y). By using Y_i as a year code, the year-specific time trend on capture probabilities was of the form logit $(p_i) = a + b \cdot Y_i$.

Survival rates in capture–recapture models are apparent survival probabilities, and $\phi = S(F)(1 - L)$, where F (fidelity) is the probability that a fish returns to (or stays in) the river reach being sampled and L is the probability of tag loss. Because PIT tag loss or failure is minimal (Burdick and Hamman 1993), L is likely to be close to zero. Thus, if F is near 1, then ϕ is an estimator of physical survival rate (S), and $1 - S$ is the total mortality rate.

Abundance and recruitment estimation.—Data were too sparse to get useful occasion-specific estimates of population size based on open-model methods (such as with program JOLLY; Pollock et al. 1990). However, by grouping sampling periods into sets of three passes within a year, the design corresponded closely enough to the robust design (Pollock 1982) that closed-model capture–recapture methods could be used to estimate population abundance each sample year. This analysis assumes population closure over a time period of about 6 weeks. The simplest model (the null model) of program CAPTURE (White et al. 1982) was used to get an abundance estimate ($\hat{N}$) by year. This model assumes the same p applies at each capture occasion within year, but p can vary by year since the estimates were done separately. The choice of this model was partly based on analyses with SURGE that supported constant within-year p, partly motivated by the sparseness of the data, and supported by the model selection algorithm in CAPTURE that suggested the use of this simplest model for each year.

A modified open population analysis method (program RECAP; Buckland et al. 1980) was used as a consistency check for average population abundance over the four years, for average annual survival rate, and to obtain some information about average annual recruitment rate (B) into the sam-

TABLE 1.—Number of Colorado squawfish lengths available for size-frequency comparisons by year and subreach (lengths from 1974–1976 could not be partitioned by year). Recaptures within a given year were not included.

	Year							
Subreach	1974–1976	1979	1982	1991	1992	1993	1994	1995
Lower reach								
Entire	0	5	4	37[a]	32[a]	82[a]	66[a]	0
Upper reach								
Lower	0	33[a]	9	21[b]	8[b]	16[c]	13[c]	0
Middle	66[a]	7	23[d]	13[b]	32[b]	40[c]	37[c]	53[a]
Upper	0	4	23[d]	23[b]	21[b]	17[c]	21[c]	0

[a] Numbers used in the analysis.
[b] Data for 1991–1992 were pooled within subreach and used in the analysis.
[c] Data for 1993–1994 were pooled within subreach and used in the analysis.
[d] Middle and upper subreaches were pooled within year and used in the analysis.

pled population. The RECAP program was also used to compute standard errors and confidence intervals on these estimated averages by use of a nonparametric bootstrap method.

Size-frequency analyses.—To detect recent changes in age structure, size-frequency data from the Colorado River were compared with data reported from earlier studies (Seethaler 1978; U.S. Fish and Wildlife Service [USFWS], Grand Junction, Colorado, unpublished field office data files). Because capture rates differed by subreach in the upper reach, tests for differences in size distributions among the three subreaches (combined 1991–1994 data) were conducted by using the Kolmogorov–Smirnov two-sample test (K–S test).

A minimum sample of about 30 different fish was assumed necessary to develop a meaningful length-frequency histogram. Data sets were available from 1974 to 1995; however, sufficient data were not available for many years, and data from 2 to 3 years were combined when necessary to obtain an adequate sample (Table 1). The K–S tests were used to identify changes in size distributions among sampling periods. Test of proportions was used to identify changes in proportions of particular size-groups between sampling periods. Attempts were made to make sample regions and gear types consistent in data comparisons between time periods. To look for evidence of recent recruitment in the upper reach, we compared pooled 1991–1992 data with pooled 1993–1994 data for each of the three subreaches and compared middle subreach data from these years with data collected there in 1995 by the USFWS.

Catch rates.—Standard linear regression (SAS Institute 1985) was applied to numbers of fish captured during each occasion to test for a temporal trend in fish abundance. Fits of CJS models using p_T were used as an aid in interpreting these results. Catch per unit effort (CPUE) of adults (mean number of fish caught per net set) in the upper reach was also compared among years (1991–1994) as an additional means to assess temporal trends in population size. Kruskal–Wallace nonparametric analysis of variance (ANOVA) was used to test for differences in CPUE among years.

Reproductive success.—Samples of age-0 and larval fish were collected (1986 through 1994) to monitor annual reproductive success of Colorado squawfish and distribution of young in the middle and upper subreaches (Grand Valley) of the upper reach. This study area was subdivided into 18 3.2-km sections with one sample of larvae collected weekly from each section during early to mid-July through August. Samples were collected from backwater, embayment, or shoreline habitats with a 0.6-m-wide, 0.5-mm-mesh, hand seine. Sampling locations within each section changed weekly, and although sampling effort was not constant among sites (5–15 min of seining per site), average effort per site was assumed constant among years.

Age-0 Colorado squawfish were sampled once yearly in late September or early October by seining backwaters with a 4.6-m-wide, 3-mm-mesh, beach seine. The middle and upper subreaches were subdivided into 8-km sections and two samples were collected from each of two backwaters within each section.

Samples of both larval and age-0 fish were preserved in 10% formalin and sent to the Larval Fish Laboratory at Colorado State University for identification. Because of the nonnormal distribution of fish captures, CPUE was calculated as a geometric mean. Kruskal–Wallis one-way ANOVA (K–W ANOVA) and Kruskal–Wallis multiple-comparison z-value tests were used to test for differences in CPUE among years.

Results

Adult Survival Rate, Abundance, and Recruitment Estimates

Upper reach.—The two best models (lowest AIC values), differing by only 0.034 AIC units, provided annual survival rate estimates ($\hat{\phi}$) of 0.845 and 0.860. The best model as determined by

TABLE 2.—Capture–recapture open models fit to the Colorado squawfish capture data. Also shown are the number of estimable parameters in each model (K), AIC (Akaike's Information Criterion) values and AIC increments (ΔAIC) compared to the AIC best model, sorted by AIC value, smallest (best model) to largest AIC (worst model).

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

AIC (Table 2) had constant capture rate on each occasion ($\hat{p}$ = 0.107, SE = 0.014), survival rate set to 1 in the short periods among sampling occasions in the spring, and constant survival ($\hat{\phi}$ = 0.845, SE = 0.076) the remaining portion of the year. The next best model, with constant survival all year ($\hat{\phi}$ = 0.860, SE = 0.069, 95% confidence interval [CI] = 0.662–0.950 based on logistic transformation) and constant capture rate, was more credible biologically because some natural mortality probably occurred during the late-April–mid-June sample periods.

To assess whether the sampled population was stable, increasing, or decreasing during the four years of study, it was important to consider models with time trends in capture rates. The best of these models were those with constant survival and logit-p having a linear trend over time (by sample occasion or by year). For model $\{\phi, p_Y\}$, $\hat{\phi}$ = 0.841 (SE = 0.072) and $\hat{p}_Y$ = 0.093 (SE = 0.020), 0.102 (SE = 0.015), 0.112 (SE = 0.015), and 0.123 (SE = 0.023) for 1991, 1992, 1993, and 1994, respectively, suggesting a 10% annual rate of increase in capture probabilities. This increase was not statistically significant (z-test = 0.914, P = 0.3607, two-sided test), as corroborated by the small ΔAIC value (1.2). Still, in judging possible increases in the sampled population based on more fish caught in later years, it would be conservative to consider that the efficiency of capturing fish may have increased 10% per year.

It seemed appropriate to use closed models to estimate population size separately by year because estimated survival rates using model $\{\phi_{\text{short; long}}, p\}$ during the short time period between cap-

TABLE 3.—Yearly population size estimates ($\hat{N}_i$) for the upper reach, based on model M_0 (constant within-year capture rates) from program CAPTURE[a]. Also shown are theoretical SEs (in parentheses) and 95% confidence intervals (profile likelihood) by year. For mean abundance, the SE is empirical and the confidence interval is based on a shifted log transform and a t_3 distibution. Capture rate estimates ($\hat{p}$) from CAPTURE are also shown.

Year i	$\hat{N}_i$ (SE)	95% confidence interval	$\hat{p}$
1991	205 (68)	124–520	0.106
1992	311 (125)	179–1204	0.074
1993	163 (29)	121–246	0.194
1994	332 (90)	223–728	0.103
Mean	253 (41)	161–440	

[a] White et al. (1992).

tures were about 0.99. Table 3 gives the results from model M_0 (constant within-year capture probabilities) computed by CAPTURE. The independent annual population size estimates are too imprecise for assessing trends, and an average for the four years was calculated as $\hat{N}$ = 253 (SE = 41, 95% CI = 161–440). The program RECAP was also used to estimate annual population size as well as annual survival and recruitment: $\hat{N}$ = 263 (SE = 38, 95% CI = 186–333); $\hat{\phi}$ = 0.822 (95% CI = 0.611–0.922); and $\hat{B}$ = 40 (SE = 10, 95% CI = 24–59). These results, consistent with estimates from SURGE and CAPTURE, support the idea of a stable population during the four years of study while not excluding the possibility of population increase during this time.

Data summaries assessing potential trends in size of the upper reach subpopulation during 1991–1994 are presented in Tables 4 and 5. Assuming constant capture probabilities over sample occasions and years, total number of fish captured from 1991 to 1994 increased 17.1% (95% CI = 8.5–24.6%) per year (linear regression, P = 0.001, two-sided t-test, df = 10).

Mean CPUE of adults in the upper reach also steadily increased from 0.32 fish/net in 1991 to 0.69 fish/net in 1994 (Table 5). When fish were partitioned by size, the increase in CPUE was apparently the result of increasing numbers of fish less than 550 mm, which steadily and significantly increased from 0.07 fish/net in 1991 to 0.35 fish/net in 1994 (P = 0.033). Older fish greater than 550 mm increased, but not significantly (P = 0.59), from 0.25 to 0.33 fish/net. Colorado squawfish less than 550 mm made up approximately 22% of those netted in the upper reach during 1991 and accounted for 51% by 1994.

Because of this evidence of increasing popula-

TABLE 4.—Number of Colorado squawfish captured (including recaptures) in the upper reach of the Colorado River by occasion and year, the number of different individuals captured by year (M_Y), and estimated annual abundance ($\hat{N}_Y$); $\hat{p}$ is used to calculate $\hat{N}_Y$ and is explained in the text.

Occasion or variable	Year 1991	1992	1993	1994
Captures				
1	23	21	31	27
2	17	25	31	37
3	25	23	33	38
Mean	21.7	23.0	31.7	34.0
Quantities				
M_Y	59	65	78	93
$\hat{p}_Y$	0.093	0.102	0.112	0.123
$\hat{p}(M_Y)$	0.254	0.276	0.300	0.325
$\hat{N}_Y$[a]	232	236	260	286

[a] Mean $\hat{N}_Y = 254$ for 1991–1994.

TABLE 5.—Mean catch per unit effort (CPUE) of Colorado squawfish captured in trammel nets (by year) in the upper-reach study area of the Colorado River; CPUE = number of fish caught per net; N = number of nets set; TL = total length.

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

tion size and capture probabilities in the upper reach, annual abundance (N_Y) was computed by assuming increases in both abundance and capture probabilities during 1991–1994. If M_Y is the number of distinct fish captured by year, the probability of catching a fish (once or more) present in a year is $\hat{p}(M_Y) = 1 - (1 - \hat{p}_Y)^3$, where $\hat{p}_Y$ is from the open model $\{\phi, p_Y\}$. The best estimator of abundance by year allowing this trend in capture rates is thus $\hat{N}_Y = M_Y/\hat{p}(M_Y)$; these estimates, averaging 254 but reflecting an increase in abundance from 1991 to 1994, are shown in Table 4.

Lower reach.—Estimates in the lower reach included not only adults, as in the upper reach, but also subadults as small as 250 mm. However, the vast majority of captures were of individuals longer than 300 mm (see section below on size frequency). Size bias from switching to a finer-mesh net after 1991 in the lower reach was probably minimal: only two fish smaller than 259 mm (the smallest captured with the larger-mesh net) were subsequently captured with the finer net.

Results from CAPTURE using model M_t for the 3 years with two within-year sampling passes were $\hat{N} = 224$ (SE = 155) for 1992, $\hat{N} = 512$ (SE = 228) for 1993, and $\hat{N} = 297$ (SE = 126) for 1994; the average estimate for the 3-year period was $\hat{N} = 344$ (SE = 101, 95% CI = 196–604). Program RECAP provided an estimate of average abundance over the 3-year period (1992–1994) in the lower reach of $\hat{N} = 425$ (SE = 144, 95% CI = 196–732). However, because RECAP assumes that time intervals between occasions are all equal (within-year intervals were similar to each other but were not similar to among-year intervals), some nonoptimal weighting occurred when the program averaged across years. A better weighting produced an estimate of $\hat{N} = 385$ (SE = 130, 95% CI = 202–733). From RECAP, there was indication of recruitment over the 3-year period (average $\hat{B} = 118$, SE = 74), but abundance estimates suggest that sizable recruitment occurred only between 1992 and 1993 with an increase of several hundred fish.

Survival estimates for the lower reach were calculated from SURGE ($\hat{\phi} = 0.57$, 95% CI = 0.34–0.95) and RECAP ($\hat{\phi} = 0.43$, 95% CI = 0.15–0.78). Because of wide standard errors, neither estimate is particularly useful; however, both estimates indicated a considerably lower apparent survival rate for the lower reach than for the upper reach. This would be consistent with fish emigrating from the lower reach if their actual physical survival was similar to that of fish in the upper reach, or it could actually represent higher mortality.

Size Frequency: Lower Reach

A relatively large number of subadults was found in the lower reach during 1991, and growth and distribution of this group was subsequently tracked through 1994 (Figure 1). Scale analysis indicated this pulse of subadult fish was composed

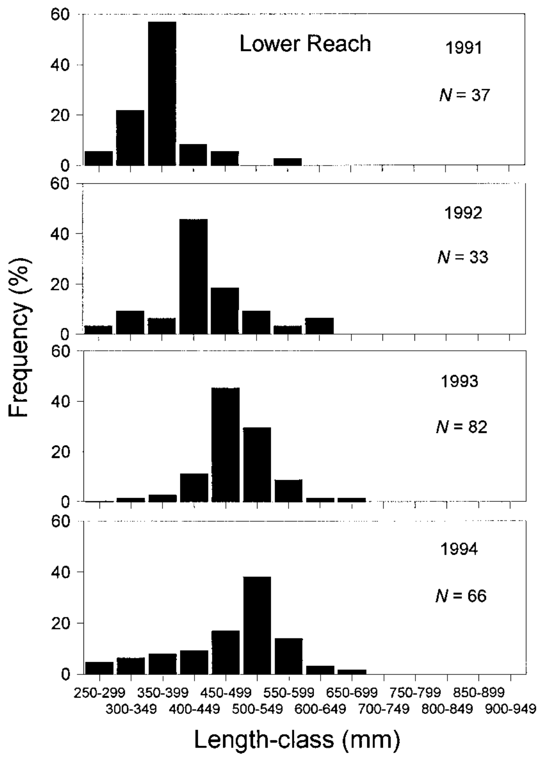

FIGURE 1.—Length distributions of Colorado squawfish captured (N) in the lower reach of the Colorado River during 1991–1994.

of three consecutive year-classes, which exhibited much overlap in fish lengths (Table 6). Subsamples from fish of this group captured in 1991 (N = 15, 259–383 mm) and 1992 (N = 22, 307–479 mm) were aged by using scale analysis (see Osmundson et al. 1997 for methods), and 22% had hatched in 1985, 46% in 1986, 27% in 1987, and 5% in 1988. These results suggest a strong year-class was produced in 1986 and perhaps also in 1985 and 1987.

There were few fish present in the lower reach during 1991–1994 that were larger (older) or smaller (younger) than individuals from the 1985–1987 year-classes (Figure 1). This group dominated the lower river subpopulation during the study period. This suggests that no similarly strong year-classes were produced for at least 3 years prior to 1985 and that none were produced for at least 3 years after 1987. These findings were consistent with those of McAda et al. (1994), who found that spring electrofishing catch rates had been relatively low in this portion of the river during 1986–1990. In addition, relatively low catch rates back to 1986 suggest that no large pulse of young fish was produced since at least 1977.

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

Year collected	Length (mm)	N	Age (years)	Year-class
1991	259	1	3	1988
	325–374	3	4	1987
	332–383	9	5	1986
	375–379	2	6	1985
1992	307	1	4	1988
	326–452	7	5	1987
	412–472	8	6	1986
	430–479	6	7	1985

Size Frequency: Upper Reach

Comparisons among subreaches.—Size distribution (combined 1991–1994 data) of upper-subreach fish (Figure 2) was significantly different from that of middle-subreach fish (P = 0.003, K–S test) and that of lower-subreach fish (P = 0.0002, K–S test); size distributions of middle- and lower-subreach fish were not significantly different (P = 0.11, K–S test).

Comparisons of earlier years with recent years.—Only one significant difference was found in comparisons among length-frequency distributions of recent and earlier years within the three

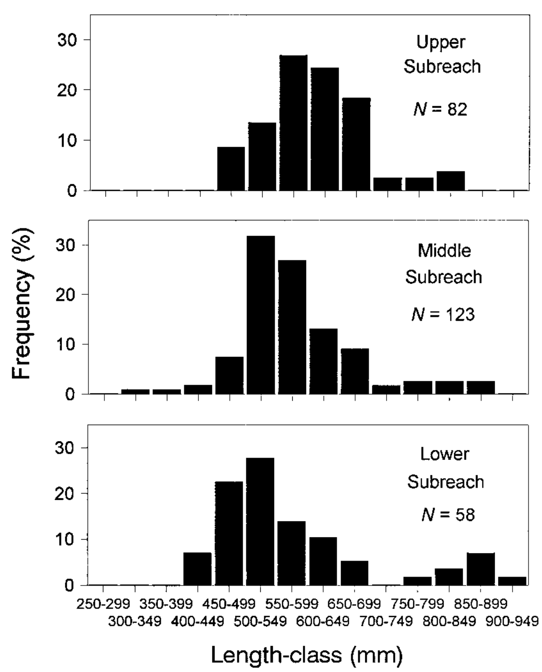

FIGURE 2.—Length distributions of Colorado squawfish captured (N) in the upper, middle, and lower subreaches of the upper reach of the Colorado River during 1991–1994 (yearly data pooled).

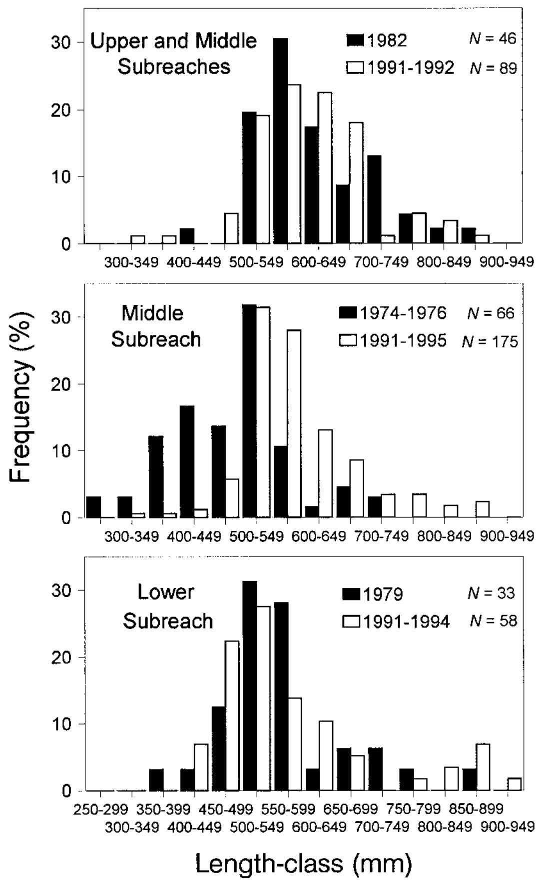

FIGURE 3.—Length distributions of Colorado squawfish captured (N) during recent and earlier surveys. Reaches and years were pooled as shown (see Table 1) to meet sample size objectives (>30 fish per distribution) and to keep sampling gear types consistent among time periods.

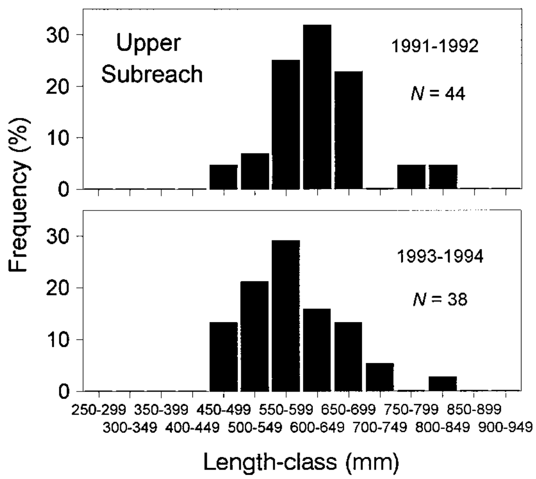

FIGURE 4.—Length distributions of Colorado squawfish captured (N) in the upper subreach of the upper reach during 1991–1992 and 1993–1994.

subreaches of the upper reach: this was between the distributions of the combined 1974–1976 period and the combined 1991–1995 period (Figure 3, middle panel) in the middle subreach (P = 0.00001, K–S test). The proportion of captured fish less than 550 mm was significantly greater (P = 0.00001, test of proportions) for 1974–1976 than for recent years, and many of the fish (35%) were less than 450 mm during 1974–1976. The highest proportion of fish less than 450 mm in recent years was 10% in the lower subreach during 1991–1992 (data not shown). Comparisons between distributions in other years (Figure 3, top and bottom panels) failed to indicate significant differences ($P >$ 0.05, K–S test) between early and recent periods.

Comparisons among recent years.—In the upper subreach of the upper reach, fish 600–649 mm were the most abundant group during 1991–1992, but a significant change (P = 0.03, K–S test) in size distribution to smaller fish in 1993–1994 occurred, and the 550–599-mm size-class became dominant (Figure 4). In addition, the proportion of fish less than 550 mm significantly increased (P = 0.01, test of proportions) between 1991–1992 and 1993–1994, which would be consistent with an influx of young fish from the lower reach.

In the middle subreach, differences in size distribution were significant only between 1993–1994 and 1995 (P = 0.02, K–S test): in 1995 there was a smaller proportion of fish less than 500 mm (P = 0.04, test of proportions). Comparisons between individual years also indicated a difference between size distributions in 1994 and 1995 (P = 0.04, K–S test): the proportion of fish less than 550 mm declined between 1994 and 1995 (P = 0.02, test of proportions).

In the lower subreach, size distributions did not significantly change (P = 0.80, K–S test) between 1991–1992 and 1993–1994. An apparent increase in the proportion of fish captured in the 450–499-mm length-class from 17% (1991–1992) to 28% (1993–1994) was not significant (P = 0.34, test of proportions).

Reproductive Success

Results from seining surveys indicated that 1986 and perhaps 1987 were comparatively good years for Colorado squawfish reproduction in the upper reach. No larval or age-0 fish were collected from the upper subreach during the 1986–1994 study period, though one yearling-sized individual (105 mm) was captured there in 1986. Larvae were collected from the middle subreach (1–8 fish annually) during 6 of the 9 years. All were collected downstream of rkm 263.5. In 1986, one larva was also collected from the lower 3.5 km of the Gunnison River. The highest number of larvae collected from the middle subreach was in 1986; however, differences in mean CPUE among years (Figure 5) were not significant ($\chi^2 = 9.24$, $P = 0.32$, df = 8, K–W ANOVA). Age-0 Colorado squawfish were captured (1–29 fish annually) from the middle subreach also during 6 of the 9 years; all were captured downstream of rkm 262.7. Mean CPUE was significantly different among years ($\chi^2 = 27.08$, $P < 0.0007$, df = 8) with 1986 being the only year significantly higher than others ($P < 0.05$). Though CPUE in 1987 appeared higher than in subsequent years, the difference was not significant ($P > 0.05$). These results for age-0 fish were similar to those of McAda et al. (1994) for the lower reach, where mean CPUE for 1986 was double that of any other year (1986–1992). Earlier, riverwide surveys of age-0 Colorado squawfish by the USFWS, extending back to 1982, indicated an even higher CPUE in 1985 than in 1986 (McAda and Kaeding 1989).

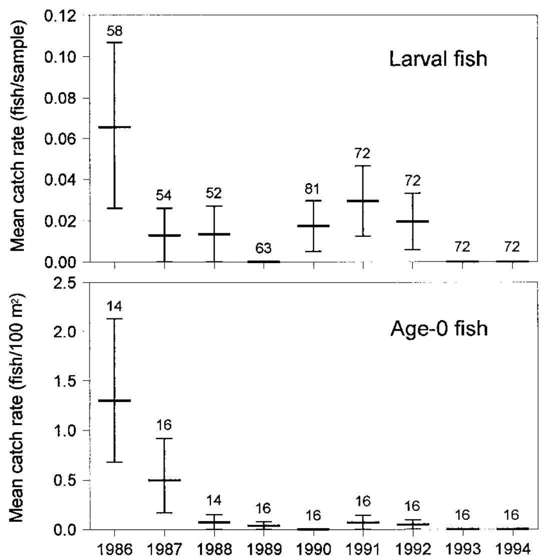

FIGURE 5.—Annual catch per unit effort (±SE) of larval (top) and age-0 (bottom) Colorado squawfish in the middle subreach from 1986 through 1994. Catch rates are geometric means; sample size is reported above SE bars.

Discussion

Demographics

The best point estimate of abundance of adult Colorado squawfish in the upper reach during 1991–1994 was about 250 fish; in the lower reach, the best point estimate was about 350 fish. Although sizable variability was associated with these estimates, different estimators produced similar point estimates. Many individuals in the lower reach subpopulation appeared to be part of 1–3 strong year-classes spawned in the mid-1980s, and an increasing trend in the upper-reach subpopulation during 1991–1994 resulted from upstream movements of these cohorts (see Osmundson et al. 1998). At the beginning of this study, very few adult-sized fish were captured in the lower reach. Thus, the 250 adult fish in the upper reach might have represented the bulk of the breeding population of the entire river until this pulse of new fish recruited to adulthood. This census number indicates an effective population size (N_e; usually considerably less than the census or actual population size) well below thresholds suggested for maintaining adaptive genetic variance for long-term population viability: 5,000 suggested by Lande (1995) or 500 by Franklin (1980) and Soule (1980).

The best point estimate of annual survival of adult Colorado squawfish in the upper reach (0.86) was very similar to the survival rate for Colorado squawfish greater than 550 mm (0.85) estimated by Osmundson et al. (1997) using a different approach. Though both methods used the same capture records, estimates here were based on capture–recapture histories whereas Osmundson et al. (1997) used a modified Chapman–Robson (Seber 1982) model where survival is based on declining numbers of increasingly older individuals. Though estimates in both studies were higher than one reported by Gilpin (1993) for the Green River population (0.81), actual differences between populations may be small: Gilpin's sensitivity analysis indicated that an overestimate in his growth calculations would have resulted in underestimating adult survival rate. In other words, if adult growth averaged 10 mm in length per year (as previously estimated by Tyus 1988) instead of the 15 mm estimated by Gilpin (1993), his survival rate estimate would increase to 0.87. In both rivers, adult survival is relatively high and therefore probably not a major constraint on population increase.

Length frequencies of adult Colorado squawfish differed between the upper and lower reaches, with larger (>500 mm) fish predominant in the upper reach. Length frequencies in the lower reach, however, were skewed by the large year-classes that materialized as subadults in 1991 and dominated the 500–549-mm size-class by 1994. The dynamic nature of these large cohorts made definitive size-frequency comparisons between reaches difficult. However, larger fish were clearly more prevalent in the upper reach: fish longer than 600 mm were rarely caught in the lower reach, but they constituted more than 30% of captures in the upper reach. Osmundson et al. (1997) indicated that length-frequency distributions for adults longer than 550 mm in the upper reach were relatively stable during 1991–1994.

Though some reproduction and recruitment may occur every year, strong year-classes are evidently infrequent. The distinct pulse of subadult fish detected in the lower reach in 1991 was distributed throughout the river within a few years. This infusion of new fish into the population was apparently the result of one or more strong year-classes produced during the mid-1980s, a phenomenon corroborated by catch rates of larvae and young of year during those years. Given that high reproductive success later resulted in strong recruitment (at least to size-classes up to 550 mm), low numbers of adult Colorado squawfish in the Colorado River may be a result of insufficient reproductive success during most years.

The degree of reproductive success and first-year survival is probably determined by environmental conditions that vary yearly rather than by fluctuations in size of the spawning population (i.e., egg output), because apparent increases in adult numbers during the 4 years of this study did not result in concomitant increases in catch rates of larvae or age-0 fish during the same time period. Conversely, weak year-classes beginning in 1988 followed the relatively strong year-classes of 1985 through 1987, while the number of adults probably changed little. A significant environmental factor that may affect reproductive success is the magnitude of spring flows: McAda and Kaeding (1989), Osmundson and Kaeding (1991), and McAda et al. (1994) found significant positive correlations between fall catch rates of age-0 Colorado squawfish in the Colorado River and the magnitude of spring flows that preceded the spawning season. Exceptionally high flows may also be a precursor to successful reproduction because the strong year-classes of 1985–1987 were preceded by extremely high spring flows during 1983–1984.

Demographic Trends

Comparisons with historical abundance are difficult because of the paucity of biological studies or surveys conducted prior to the 1970s. Jordan (1891) conducted surveys in the upper Colorado River basin in 1889 and later described (Jordan and Evermann 1896) abundance and distribution of Colorado squawfish as, ''Colorado Basin, very abundant in the river channels as far north as the base of the Rocky Mountains in Colorado (Uncompahgre River at Delta).'' Compiled accounts and photographs collected by Quarterone (1993) of Colorado River fish during the first half of this century also indicate much higher abundance of Colorado squawfish in the upper Colorado River than observed in this study (or studies dating back to the early 1970s). Differences in abundance from these historic accounts and current estimates strongly suggest that the long-term population trend has been downward.

Because of the longevity of Colorado squawfish and their pulsed recruitment, the significance of short-term trends in abundance is difficult to evaluate. Our study coincided with a period when recruitment to the adult population was comparatively high and overall numbers of adults appeared to increase. However, a longer time frame must be considered when evaluating trends of long-lived species, especially one with such a long lag-time between hatching and recruitment to the adult population. Although the 1985–1987 year-classes might have recently increased the size of the adult population, reproductive success since 1987 has been relatively low, and the trend of increase in adults could be reversed in the near future.

Major trends were not observed in length-frequency distributions of adult Colorado squawfish in the upper reach. However, a difference in length frequency of fish longer than 250 mm was observed in the middle subreach of the upper reach between the 1974–1976 period and this study (Figure 4), suggesting a decrease in the proportions of juveniles and subadults in the upper reach during the past 20 years. More than one-third of the fish in this subreach during 1974–1976 were 250–450 mm. The rarity of individuals shorter than 450 mm in the upper reach today, coupled with the stable length distribution of adults greater than 550 mm, suggests that upper-reach recruitment presently comes from the lower reach. In addition, most individuals evidently do not move to the upper reach until they have attained a length of more than 450 mm (Osmundson et al. 1998). Two hypotheses may explain this change in the upper-reach, length-frequency distribution: (1) nursery habitat in the upper reach was formerly of higher quality and quantity than in later years, and a smaller proportion of larvae drifted to the lower reach, and (2) reproduction or hatching success in the upper reach was formerly much greater than that today, and substantial numbers of larvae were retained in the upper reach even though proportions drifting to the lower reach might have been similar to those in recent years.

Status and Future Prospects

This work and that of others strongly suggest that the population of Colorado squawfish in the Colorado River is small but actively recruiting new individuals to the adult population. Whether population size is relatively constant over time is difficult to ascertain, but abundance is apparently much less than that reported earlier in this century. Strong year-classes augment the population enough to cause observable changes in population structure and abundance. The significance of these large year-classes in maintaining the adult population is also difficult to ascertain, but the apparent increase in numbers of adults observed during this study suggests that the infrequency of recruitment pulses currently limits the size of the adult population.

Metapopulation theory argues that stochastic fluctuations cause local extinctions, and the probability of extinction decreases with increased population size. Thus, to minimize the probability of being driven to extinction, the goal is to achieve a population size large enough to withstand stochastic fluctuations and also to maintain sufficient genetic diversity (see Soule 1986; Simberloff 1988). Crossing over from the Green River does occur at some unknown rate: the first documented case was an individual caught at Green River rkm 52.5 in 1994 and recaptured in the lower Gunnison River (rkm 3.5) in 1996 (B. Burdick, USFWS, personal communication; T. Chart, Utah Division of Wildlife Resources, personal communication). Such movement, even at a low rate (1–10/generation), should alleviate genetic problems associated with small population size (see Franklin 1980; Gilpin 1993; Mills and Allendorf 1996); therefore, stochastic demographic fluctuations are probably a greater threat to this small population.

The abundance of age-0 fish and subsequent recruitment is probably the greatest source of demographic fluctuation in the population of Colorado squawfish in the Colorado River. If population size and viability is limited by this recruitment, then strong year-classes are needed more frequently. Presently, variables controlling the relative success of annual reproduction and first-year survival are not clearly understood. However, if spawning and hatching success are linked to conditions created by spring runoff, changes in runoff patterns in the Colorado River during the past half century resulting from water development may in part explain the decline of this population.

A greatly reduced frequency of high spring runoff flows (Osmundson and Kaeding 1991; Van Steeter 1996) influences four factors that might have negatively affected this population. First, high flows during spring may be required to create fresh cobble bars for spawning (Harvey et al. 1993) and adequately cleanse fines from existing bars (Haynes et al. 1984; Reiser et al. 1989), conditions apparently necessary for spawning site selection by both the northern squawfish *P. oregonensis* (now northern pikeminnow; Nelson et al. 1998) and Colorado squawfish (Beamesderfer and Congleton 1981; Lamarra et al. 1985). The existence of interstitial voids for protection of deposited eggs and creation of microcurrents among voids for successful egg incubation may contribute to high egg-hatching success. Second, high flows may serve to dilute waterborne contaminants from agricultural and urban sources that may interfere with reproductive behavior, reduce egg viability, or reduce larval survival (Woodward et al. 1985; Hamilton and Waddell 1994). Third, river bottomlands require periodic high flows to maintain channel (and thus habitat) diversity and biological productivity (Junk et al. 1989; Bayley 1991; Rasmussen 1996) important to young Colorado squawfish. Finally, high, sustained spring flows serve to reduce numbers of nonnative minnows that now dominate backwater nursery habitats (McAda and Kaeding 1989; Osmundson and Kaeding 1991; Muth and Nesler 1993; Gido et al. 1997). Although a food source for subadult Colorado squawfish, the prolific red shiner *Cyprinella lutrensis* preys on Colorado squawfish larvae (Ruppert et al. 1993), and larvae of fathead minnow *Pimephales promelas* compete with Colorado squawfish larvae for food (Beyers et al. 1994).

Low adult numbers and infrequent, pulsed recruitment make this population vulnerable to extirpation over time. Natural variation in demographics alone makes viability of this population tenuous, even if stability of habitat conditions is assumed. However, for many imperiled species, the threat of deterministic habitat change is probably greater than stochastic demographic variation (Caughley 1994; Harcourt 1995). This may be especially true for this population: more water depletions are planned, more nonnative species may be introduced, and floodplains may continue to constrict from construction of additional jetties and dikes and from further channel-stabilizing effects of exotic riparian vegetation (see Graf 1978).

Colorado squawfish, with their exceptional longevity (Osmundson et al. 1997) and high fecundity (Hamman 1986), are well equipped to persist through long periods of adverse conditions. Historically, their basinwide distribution no doubt provided adequate colonization sources if drought or other conditions temporarily rendered one or more tributaries uninhabitable. Today, habitat modifications occur rapidly and are likely to persist for long periods; in addition, colonization sources have been substantially reduced. Though the nearby Green River population may serve as a colonization source for the Colorado River (Gilpin 1993), a balance between local extinction and colonization (see Gilpin and Hanski 1991) for this and other wild populations is unlikely if extinction is caused by a deterministic response to degraded habitat conditions (Harrison 1991; Thomas 1994). The same logic applies to stocking hatchery-reared Colorado squawfish to reestablish extirpated populations. Recovery to a viable, self-sustaining level depends on first identifying and then ameliorating or eliminating the ultimate limiting factors (Tear et al. 1995).

For this population, a low frequency of strong year-classes currently appears to limit adult abundance. Although any increase in adult survival rate would be beneficial, the success of recovery efforts will largely depend on providing environmental conditions that increase reproductive success and survival of early life stages.

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References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.

Anderson, D. R., K. P. Burnham, and G. C. White. 1994. AIC model selection in over dispersed capture–recapture data. Ecology 75:1780–1793.

Anderson, R. O., and S. J. Gutreuter. 1983. Length, weight, and structural indices. Pages 283–300 *in* L. A. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Bayley, P. B. 1991. The flood pulse advantage and the restoration of river–floodplain systems. Regulated Rivers: Research and Management 6:75–86.

Beamesderfer, R. C., and J. L. Congleton. 1981. Spawning behavior, habitat selection, and early life history of northern squawfish with inferences to Colorado squawfish. Pages 47–127 *in* Part 3, Colorado River Fishery Project, Final Report. U.S. Fish and Wildlife Service and Bureau of Reclamation, Contracted Studies, Salt Lake City, Utah.

Belknap, B., and B. Belknap. 1974. Canyonlands river guide. Westwater Books, Belknap Photographic Services, Boulder City, Nevada.

Beyers, D. W., R. T. Muth, and M. S. Farmer. 1994. Experimental evidence of competition between larvae of Colorado squawfish and fathead minnow. Colorado State University, Larval Fish Laboratory, Final Report, Fort Collins.

Buckland, S. T. 1980. A modified analysis of the Jolly–Seber capture–recapture model. Biometrics 36:419–435.

Burdick, B. D., and R. L. Hamman. 1993. A study to evaluate several tagging and marking systems on the Colorado squawfish, razorback sucker, and bonytail. U.S. Fish and Wildlife Service, Final Report, Grand Junction, Colorado.

Burnham, K. P., and D. R. Anderson. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. Pages 16–30 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier, London.

Burnham, K. P., D. R. Anderson, and G. C. White. 1996. Meta-analysis of vital rates of the northern spotted owl. Studies in Avian Biology 17:92–101.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society, Monograph 5, Bethesda, Maryland.

Burnham, K. P., G. C. White, and D. R. Anderson. 1995. Model selection strategy in the analysis of capture–recapture data. Biometrics 51:888–898.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. Wagner. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. Studies in Avian Biology 17: 12–20.

Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135–149 *in* M. E. Soule and B. A. Wilcox, editors. Conservation biology: an evolutionary–ecological perspective. Sinauer, Sunderland, Massachusetts.

Gido, K. B., D. L. Propst, and M. C. Molles. 1997. Spatial and temporal variation of fish communities in secondary channels of the San Juan River, New Mexico and Utah. Environmental Biology of Fishes 49:417–434.

Gilpin, M. 1993. A population viability analysis of the Colorado squawfish in the upper Colorado River basin. Report of University of San Diego, Department of Biology, to U.S. Fish and Wildlife Service, Denver.

Gilpin, M., and I. Hanski, editors. 1991. Metapopulation dynamics: empirical and theoretical investigations. Academic Press, London.

Graf, W. L. 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. Geological Society of America Bulletin 89:1491–1501.

Hamilton, S. J., and B. Waddell. 1994. Selenium and milt of razorback sucker (*Xyrauchen texanus*) in the middle Green River, Utah. Archives of Environmental Contamination and Toxicology 27:195–201.

Hamman, R. L. 1986. Induced spawning of hatchery-reared Colorado squawfish. Progressive Fish-Culturist 48:72–74.

Harcourt, A. H. 1995. Population viability estimates: theory and practice for a wild gorilla population. Conservation Biology 9:134–142.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42:73–88.

Harvey, M. D., R. A. Mussetter, and E. J. Wick. 1993. Physical process-biological response model for spawning habitat formation for the endangered Colorado squawfish. Rivers 4:114–131.

Haynes, C. M., T. A. Lytle, E. J. Wick, and R. T. Muth. 1984. Larval Colorado squawfish *(Ptychocheilus lucius* Girard) in the upper Colorado River basin, Colorado, 1979–1981. Southwestern Naturalist 29:21–33.

Jordan, D. S. 1891. Report of explorations in Colorado and Utah during the summer of 1889, with an account of the fishes found in each of the river basins examined. U.S. Fish Commission Bulletin 9(1889).

Jordan, D. S., and B. W. Evermann. 1896. The fishes of North and Middle America. U.S. National Museum Bulletin 47:Part 1.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river–floodplain systems. Pages 110–127 *in* D. P. Dodge, editor. Proceedings of the international large river symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106:31–48.

Lamarra, V. A., M. C. Lamarra, and J. G. Carter. 1985. Ecological investigation of a suspected spawning site of Colorado squawfish on the Yampa River, Utah. Great Basin Naturalist 45:127–140.

Lande, R. 1995. Mutation and conservation. Conservation Biology 9:782–791.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: case studies and recent advances. Ecological Monographs 62:67–118.

McAda, C. W., and five coauthors. 1994. Interagency standardized monitoring program: summary of results, 1986–1992. U.S. Fish and Wildlife Service, Recovery Implementation Program, Final Report, Denver.

McAda, C. W., and L. R. Kaeding. 1989. Relations between maximum–annual river discharge and the relative abundance of age-0 Colorado squawfish and other fishes in the upper Colorado River. U.S. Fish and Wildlife Service, Final Report, Grand Junction, Colorado.

Miller, R. R. 1961. Man and the changing fish fauna of the American Southwest. Papers of the Michigan Academy of Science, Arts and Letters 46:365–404.

Mills, L. S., and F. W. Allendorf. 1996. The one-migrant-per-generation rule in conservation biology. Conservation Biology 10:1509–1518.

Moyle, P. B. 1976. Inland fishes of California. University of California Press, Berkeley.

Muth, R. T., and T. P. Nesler. 1993. Associations among flow and temperature regimes and spawning periods and abundance of young of selected fishes, lower Yampa River, Colorado, 1980–1984. Colorado State University, Larval Fish Laboratory, Final Report, Fort Collins.

Nelson, J. S., and five coauthors. 1998. Recommended changes in common fish names: pikeminnow to replace squawfish (*Ptychocheilus* spp.). Fisheries 23(9):37.

Osmundson, D. B., and five coauthors. 1998. Dispersal patterns of subadult and adult Colorado squawfish in the upper Colorado River. Transactions of the American Fisheries Society 127:943–956.

Osmundson, D. B., and L. R. Kaeding. 1989. Studies of Colorado squawfish and razorback sucker use of the ‘15-mile reach’ of the upper Colorado River as part of conservation measures for the Green Mountain and Ruedi Reservoir water sales. U.S. Fish and Wildlife Service, Final Report, Grand Junction, Colorado.

Osmundson, D. B., and L. R. Kaeding. 1991. Recommendations for flows in the 15-mile reach during October–June for maintenance and enhancement of endangered fish populations in the upper Colorado River. U.S. Fish and Wildlife Service, Final Report, Grand Junction, Colorado.

Osmundson, D. B., R. J. Ryel, and T. E. Mourning. 1997. Growth and survival of Colorado squawfish in the upper Colorado River. Transactions of the American Fisheries Society 126:687–698.

Platania, S. P., K. R. Bestgen, M. A. Moretti, D. L. Propst, and J. E. Brooks. 1991. Status of Colorado squawfish and razorback sucker in the San Juan River, Colorado, New Mexico, and Utah. Southwestern Naturalist 36:147–150.

Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture . Journal of Wildlife Management 46:752–757.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs 107.

Quarterone, F. 1993. Historical accounts of upper Colorado River basin endangered fish. Colorado Division of Wildlife, Final Report, Denver.

Rasmussen, J. L. 1996. Floodplain management: American Fisheries Society position statement. Fisheries 21(4):6–10.

Reiser, D. W., M. P. Ramey, and T. A. Wesche. 1989. Flushing flows. Pages 91–135 *in* J. A. Gore and G. E. Petts, editors. Alternatives in regulated river management. CRC Press, Boca Raton, Florida.

Ruppert, J. B., R. T. Muth, and T. P. Nesler. 1993. Predation on fish larvae by adult red shiner, Yampa and Green Rivers, Colorado. Southwestern Naturalist 38:397–399.

SAS Institute. 1985. SAS language guide for personal computers, version 6 edition. SAS Institute, Cary, North Carolina.

Seber, G. A. F. 1982. The estimation of animal abundance. Macmillan, New York.

Seethaler, K. H. 1978. Life history and ecology of the Colorado squawfish (*Ptychocheilus lucius*) in the upper Colorado River basin. Master's thesis. Utah State University, Logan.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. Annual Review of Ecology and Systematics 19:473–511.

Soule, M. E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pages 151–170 *in* M. E. Soule and B. A. Wilcox, editors. Conservation biology: an evolutionary–ecological perspective. Sinauer, Sunderland, Massachusetts.

Soule, M. E., editor. 1986. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts.

Tear, T. H., J. M. Scott, P. H. Hayward, and B. Griffiths. 1995. Recovery plans and the Endangered Species Act: are criticisms supported by data? Conservation Biology 9:182–195.

Thomas, C. D. 1994. Extinction, colonization, and metapopulations: environmental tracking by rare species. Conservation Biology 8:373–378.

Tyus, H. M. 1988. Long-term retention of implanted transmitters in Colorado squawfish and razorback suckers. North American Journal of Fisheries Management 8:264–267.

Tyus, H. M. 1991. Ecology and management of Colorado squawfish. Pages 379–402 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction: native fish management in the American west. University of Arizona Press, Tucson.

Valdez, R. A., P. G. Mangan, R. P. Smith, and B. C. Nilson. 1982. Upper Colorado River investigation (Rifle, Colorado, to Lake Powell, Utah). Pages 100–279 *in* Part 2, Colorado River Fishery Project, Final Report. U.S. Fish and Wildlife Service and Bureau of Reclamation, Field Investigations, Salt Lake City, Utah.

Van Steeter, M. M. 1996. Historic and current processes affecting channel change and endangered fish habitats of the Colorado River near Grand Junction, Colorado. Doctoral dissertation. University of Colorado, Boulder.

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, LA-8787-NERP, Los Alamos, New Mexico.

Woodward, D. F., R. G. Riley, M. G. Henry, J. S. Meyer, and T. R. Garland. 1985. Leaching of retorted oil shale: assessing the toxicity to Colorado squawfish, fathead minnows, and two food-chain organisms. Transactions of the American Fisheries Society 114: 887–894.

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