Dispersal Patterns of Subadult and Adult Colorado Squawfish in the Upper Colorado River

D. B. Osmundson*

U.S. Fish and Wildlife Service, Colorado River Fishery Project
764 Horizon Drive, South Annex A, Grand Junction, Colorado 81506-3946, USA

R. J. Ryel

Utah State University, Department of Rangeland Resources, Logan, Utah 84322-5230, USA

M. E. Tucker[1] and B. D. Burdick

U.S. Fish and Wildlife Service, Colorado River Fishery Project

W. R. Elmblad

Colorado Division of Wildlife, 711 Independent Avenue, Grand Junction, Colorado 81505, USA

T. E. Chart

Utah Division of Wildlife Resources, 1165 South Highway 191, Suite 4, Moab, Utah 84532, USA

Abstract.—We investigated distribution and dispersal patterns of subadult and adult Colorado squawfish *Ptychocheilus lucius* (recently renamed the Colorado pikeminnow) throughout their range in the upper Colorado River. Annual, river-wide, capture–recapture data were used to document movements during a 5-year period (1991–1995). Average total length of Colorado squawfish progressively increased upstream: juveniles and subadults occurred almost exclusively in the low-ermost 105 km of the 298-km study area, whereas most adults were concentrated in the uppermost 98 km. This was most pronounced early in the study and less so later due to the effect of two or three strong year-classes that dispersed through the system. Only 16% of subadult and adult fish initially captured and tagged in the upper reach were later located more than 10 km from the previous capture site; of those tagged in the lower reach, 58% were later located more than 10 km from the previous site. Most movements greater than 10 km were directed upstream, and many fish tagged in the lower reach moved to the upper reach; the smallest of these fish was between 421 and 449 mm in total length (TL) when it moved. No movement was detected from the upper reach to the lower. Distance moved was inversely related to fish size: displacement of fish shorter than 550 mm TL averaged 33.6 km; for those longer than 550 mm, average displacement was only 7.5 km. Movement of young adults may have been a response to changing food needs. Upstream movements placed fish into areas with greater availability of larger prey, and body condition of large adults during spring was significantly higher in the upper reach than in the lower reach. Water temperatures, however, were inversely related to adult distribution despite a preference for warmer water. We suggest that portions of the upper reach offer adults the best balance between food and water temperature.

Introduction

Understanding the life history of the endangered Colorado squawfish *Ptychocheilus lucius* (recently renamed the Colorado pikeminnow; Nelson et al. 1998) is prerequisite to developing strategies for its recovery. This warmwater piscivore, endemic to the Colorado River system and the largest cyprinid native to North America, has integrated movements into its life strategies. Annual, pota-modromous, spawning migrations (e.g., Tyus and McAda 1984; Tyus 1985, 1990; McAda and Kaeding 1991; Ryden and Ahlm 1996), and downstream drift of emerging larvae (e.g., Haynes et al. 1984; Nesler et al. 1988; Tyus 1990; Tyus and Haines 1991) have been well documented.

Longitudinal differences in fish size within the Colorado (Valdez et al. 1982; Osmundson and Burnham 1998, this issue) and Green (Tyus 1986) rivers suggest that movements may serve purposes or functions in addition to those associated with reproduction. Early life stages are found primarily in lower reaches, whereas adults are found pri-

* Corresponding author: doug_osmundson@fws.gov
[1] Present address: U.S. Fish and Wildlife Service, Northern Central Valley Fish and Wildlife Office, 10950 Tyler Road, Red Bluff, California 96080, USA.
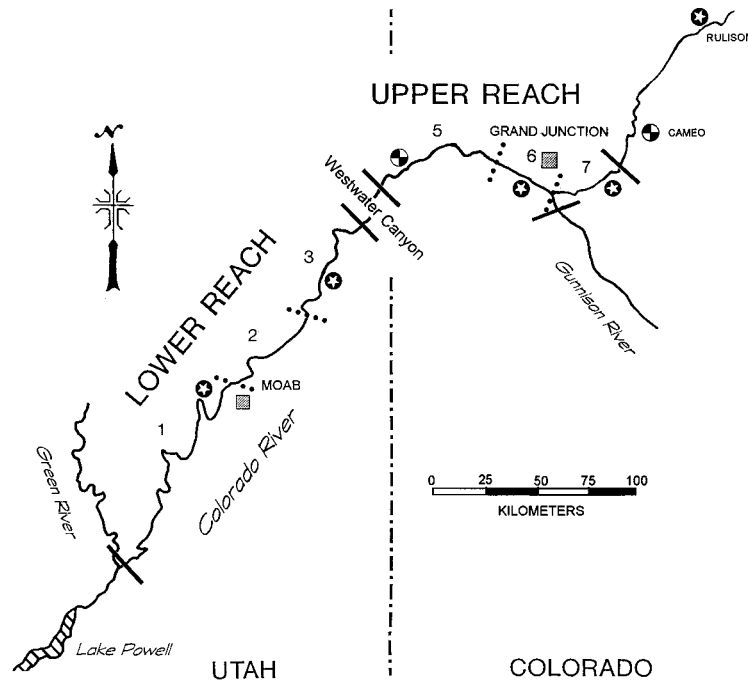
FIGURE 1.—Map of the study area. The lower boundary is the Green River confluence. Upper and lower study reaches are separated by Westwater Canyon. Also marked are the upper ends of the study area on the Colorado and Gunnison rivers where diversion dams blocked upstream movement of fish. Dotted lines demarcate the boundaries of the seven study strata (numbered). Starred circles are locations of U.S. Fish and Wildlife Service thermographs; crossed circles are locations of U.S. Geological Survey gauging stations with thermographs.

marily in more upstream reaches. The best spawning habitat ostensibly occurs in middle to upper reaches, and long-distance drift provides a mechanism for delivering emerging larvae to optimal nursery habitat, generally located far downstream (Tyus 1990). With young fish primarily in lower river reaches, higher concentrations of adults in upper reaches suggest that distribution of subadults or adults requires extensive upstream movements. To date, these movements have not been documented and factors associated with such movements are poorly understood.

Our primary objectives were to describe the distribution of subadults and adults in the Colorado River, document their dispersal patterns, and attempt to explain what motivates such dispersal. We hypothesized that upstream movement of young adults is a response to resource gradients. More specifically, we hypothesized that upstream dispersal results from individuals seeking foraging areas more likely to meet the changing food requirements of a growing piscivore, and we investigated spatial variation in Colorado squawfish body condition and abundance of likely forage

species. Longitudinal temperature gradients were also examined and related to the distribution of adults.

Methods

Study area.—The study area included the occupied range of the Colorado squawfish in the Colorado River, from the confluence with the Green River in Utah upstream to the Grand Valley diversion dam at Palisade, Colorado (the latter is a barrier to upstream movement; Figure 1). Also included was the lowermost 3.5 km of the Gunnison River, from the confluence with the Colorado River upstream to the Redlands diversion dam (also a barrier to upstream movement). Locations are in river kilometers (rkm) from the Green River confluence (rkm 0.0), converted from river miles as mapped by Belknap and Belknap (1974). The study area (Figure 1) was partitioned into a lower reach that extended from rkm 0.0 upstream to the lower end of Westwater Canyon (rkm 181.0) and an upper reach from the upper end of Westwater Canyon (rkm 200.0) upstream to the Grand Valley diversion dam (rkm 298.1). Westwater Canyon, a

TABLE 1.—Locations of study strata and subreaches sampled for potential Colorado squawfish food fishes. Locations are described in river kilometers (rkm) upstream of the confluence of the Green River. Stratum 4 was not sampled (see text).

Stratum	Mean gradient (m/km)	Strata location (rkm)	Subreach	Subreach location (rkm)
1	0.21	0.0–112.6	1	5.2–6.0
			2	12.2–13.0
			3	20.9–21.7
			4	30.1–30.9
			5	61.6–62.4
			6	100.6–101.4
			7	103.5–104.3
2	1.33	112.6–140.6	8	121.3–122.1
			9	129.0–129.8
3	0.61	140.6–181.0	10	148.5–149.3
			11	156.6–157.4
			12	172.2–173.0
4	2.42	181.0–200.0		
5	0.91	200.0–245.5	13	212.9–213.7
			14	228.0–228.8
			15	234.6–235.4
6	1.27	245.5–275.1	16	252.9–253.7
			17	270.0–270.8
7	1.70	275.1–298.1	18	287.2–288.0
			19	293.8–294.6

19-km section dominated by large rapids and turbulent eddies, was excluded for logistical reasons and because few Colorado squawfish were found there in past studies (McAda and Kaeding 1991). The river was divided into seven strata based on major changes in average channel gradient (Table 1): three downstream (strata 1–3) and three upstream (strata 5–7) of Westwater Canyon (stratum 4).

Distribution and movement.—We documented distribution of Colorado squawfish by systematically sampling the study area from mid-April through mid-June for 1991–1994. Trammel nets were set in backwaters, flooded ponds, and flooded canyon mouths because Colorado squawfish are attracted to calm habitats during the spring runoff period (Osmundson and Kaeding 1989). Capture techniques are described in detail in Osmundson and Burnham (1998). Three sampling passes (7–9 d each) through the upper reach were made each spring, and every zero- or low-velocity habitat large enough to contain adult Colorado squawfish was netted. Similar preliminary data collected during spring 1990 were also used. In the lower reach, one pass was made in 1991 and two passes were made each spring during 1992–1994. In some portions of both reaches where zero-velocity habitats were rare, shorelines were electrofished with a 5-m, electrofishing boat equipped with a Coffelt

VVP-15 electrofisher (Coffelt Manufacturing, Flagstaff, Arizona) that produced pulsed DC.

Captured Colorado squawfish were anesthetized with tricaine methanesulfonate and scanned for the presence of a passive integrated transponder (PIT) tag (Biomark, Inc., Boise, Idaho); if no tag was detected, one was implanted (see Osmundson and Burnham 1998). Fish were measured (nearest 1 mm) for maximum total length (TL; Anderson and Gutreuter 1983), weighed with an electronic balance (nearest 1 g), and released after recovery from the anesthetic.

Netting catch per unit effort (CPUE) was used to assess river-wide differences in relative abundance of adult Colorado squawfish. However, because differences in fish density among river strata may have been influenced by the number of backwaters available for use by fish (higher concentrations could occur in strata with few backwaters), we pooled netting data by reach for between-reach comparisons rather than attempt to compare densities among river strata.

To measure movement, we compared locations of consecutive captures of marked individuals. Movement patterns were compared among 100-mm length-classes and between fish initially captured in the lower reach and fish initially captured in the upper reach. Localized movements were considered to be those less than 10 km and were not analyzed. For assessing movement, we considered only consecutive captures at least 1 year apart to allow fish adequate time to disperse between captures. Also, captures during spawning periods and during pre- and postspawning migratory periods were excluded so that temporary spawning movements would not be confused with dispersal movements. Since concurrent radiotelemetry studies indicated that annual spawning movements did not commence until late June or later, only samples through 16 June were considered (except in 1994, when spawning movements began early and all June samples were excluded). Additional capture data collected during 1991–1995 by the Colorado Division of Wildlife (from stratum 5) and the Utah Division of Wildlife Resources (from portions of strata 1 and 3) were also used in the movement analysis (both agencies conduct annual spring electrofishing surveys). Records from a 1994–1995 U.S. Fish and Wildlife Service (USFWS) survey of the lower 3.5 km of the Gunnison River and a 1995 survey of flooded ponds near rkm 262 were also used.

Body condition.—Relative body condition (Le Cren 1951) was calculated for Colorado squawfish

200 mm TL and longer. Because condition changes monthly (Hawkins 1992), month-specific length–weight relationships were developed by using the 1990–1994 data. Only fishes weighed with an electronic balance were included. Excluded from the June calculations were 1994 data because we assumed gonads matured early that year and would have biased fish weights. Relative condition of each fish was calculated using the month-specific constants from the length–weight relationships (fish not weighed with a balance and those captured in June 1994 were again excluded). We compared mean condition factors between upper and lower reaches within 100-mm length-classes and among length-classes within reaches.

Relative abundance of potential forage species.—Estimates of relative abundance of small prey fish less than 100 mm TL were from unpublished fall seine survey data collected for an interagency annual monitoring program (see McAda et al. 1994 for methods). We used electrofishing and trammel netting to develop catch-rate indices of larger prey fish (>100 mm TL) likely to serve as forage for large Colorado squawfish. Electrofishing surveys were conducted from 20 April through 7 July, 1993, in two or more 0.8-km subreaches within each stratum (Table 1). The starting points (rkm) for electrofishing subreaches were selected by using a random numbers table. Within each sample subreach, both shorelines were electrofished in a downstream direction. After identification and length measurement, fish were released at the lower end of the subreach. Catch per unit effort was expressed as the number caught divided by the time electric current was applied, as metered by the VVP-15. Numbers of each species captured in trammel nets during Colorado squawfish sampling were recorded during 1992–1994, and CPUE was calculated as the mean number of fish caught per net set.

We developed an index of relative abundance for soft-rayed fusiform fish by pooling CPUE of the common species within each stratum. Spined species were excluded, as were rare species. Though prey preference of Colorado squawfish is unknown, soft-rayed fish were assumed to be preferred over spined or spiny-rayed fish, as is the case with northern pike *Esox lucius* and muskellunge *E. masquinongy* (Beyerle and Williams 1968; Mauck and Coble 1971; Wahl and Stein 1988). These two large, cool-to-warmwater, north temperate piscivores have morphologies and ecological roles similar to Colorado squawfish. Spined and spiny-rayed fish are more costly, in terms of both energy required for ingestion and risk of mortality from throat or stomach puncture (Gillen et al. 1981; McAda 1983). We conducted an additional relative abundance analysis by first partitioning potential prey so that only soft-rayed fish 100–300 mm long were considered, based on the assumption that Colorado squawfish can only consume fish up to about half their own length (e.g., Juanes 1994).

Diet.—Stomach contents of Colorado squawfish captured during 1994 were examined by using a Seaburg stomach sampler (Seaburg 1957) as modified by Gengerke et al. (1973). Back-flush tubes of various diameters were used based on the size of the fish. Empty stomachs were recorded in the field. Stomach contents from those fish containing food were preserved in 10% formalin and sent to the Larval Fish Laboratory (LFL) at Colorado State University for analysis. Food items were identified to lowest practical taxon and measured in standard length (SL), when possible; visual estimates were made of the percentage of total volume of stomach contents contributed by each taxon. The 'aggregate percent method' (Swanson et al. 1974) was used to calculate an overall percent volume for each food item for those fish containing food.

Temperature.—Main channel temperatures (nearest 0.1°C) were monitored at sites within strata 1, 3, 5, 6, and 7 and at two sites upstream of stratum 7 (Cameo and Rulison, Colorado) in a reach historically used by Colorado squawfish but presently unoccupied due to the long-term effects of three instream barriers that block migrations (Figure 1). At five sites, thermographs (Ryan Instruments, Redmond, Washington) were deployed and downloaded twice yearly. Data from stratum 5 and Cameo were collected by the U.S. Geological Survey at the Colorado–Utah state line and Cameo gauging stations, respectively. Mean daily values were calculated from readings taken every 2 h.

We compared temperature indices for growth among thermograph sites for the 1992–1996 period to measure spatial variation in thermal regime suitability along the river continuum. We derived these indices by using an approach developed specifically for Colorado squawfish by Kaeding and Osmundson (1988) in which mean daily temperatures are converted to values relative to the maximum potential (1.0) for growth at the optimum temperature (25°C); these thermal units are then summed to provide an annual value.
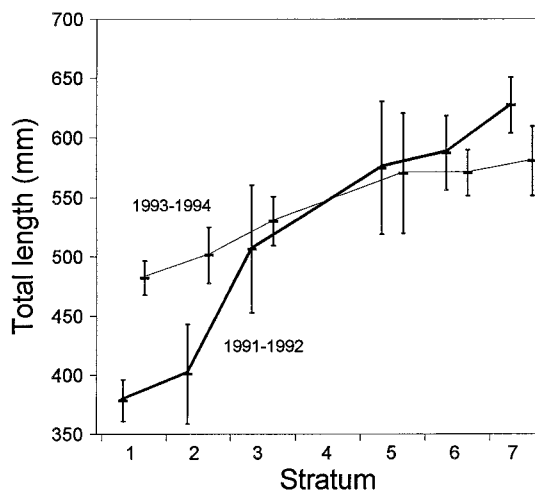
FIGURE 2.—Mean length of Colorado squawfish by stratum. Lengths of fish captured in 1991 and 1992 (heavy line) and those captured in 1993 and 1994 (light line) were pooled. Error bars represent 95% confidence intervals.

Results

Distribution

Mean length of Colorado squawfish captured in this study progressively increased upstream (Figure 2). Because samples from strata 2, 3, and 5 were small, lengths of fish captured were pooled into 1991–1992 and 1993–1994 periods for statistical tests. Analysis of variance (ANOVA) revealed that for 1991–1992 data, mean lengths in strata 3, 5, 6, and 7 differed significantly from the mean in stratum 1; those in strata 5–7 differed from the mean in stratum 2; mean lengths in strata 7 and 3 also differed ((ANOVA, Tukey–Kramer multiple comparison; $P < 0.05$). Regression indicated significant relationships (Figure 3) between total length and rkm in 1991 ($r^2 = 0.59$, $P < 0.0001$) and 1992 ($r^2 = 0.60$, $P < 0.0001$); slopes between 1991 and 1992 were not significantly different ($P = 0.28$).

For 1993–1994, differences in mean lengths among strata were not as pronounced as in 1991–1992. Significant differences were found only between stratum 1 and strata 3, 5, 6, and 7 (ANOVA, Tukey–Kramer multiple comparison, $P < 0.05$). Mean lengths in the two most downstream strata were significantly greater during 1993–1994 than during 1991–1992 (t-test, $P < 0.0001$). In the upper reach, mean lengths declined from 1991–1992 to 1993–1994 (significantly only in stratum 7; t-test, $P = 0.012$). Regression indicated significant relationships between total length and rkm loca-
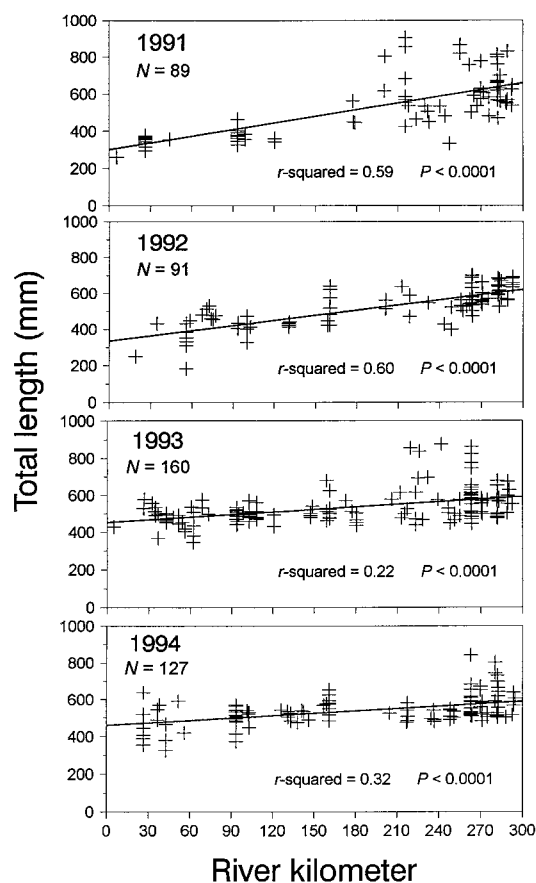

FIGURE 3.—Relationship between Colorado squawfish length and kilometers upstream from the lower end of the study area (river kilometer 0 at the Green River confluence) during 1991–1994.

tion in 1993 ($r^2 = 0.22$, $P < 0.0001$) and 1994 ($r^2 = 0.32$, $P < 0.0001$). Slopes were not significantly different between 1993 and 1994 ($P = 0.13$), but both differed from slopes of relationships for 1991 and 1992 (all $P < 0.003$).

Netting catch rates indicated that adult distribution changed during 1991–1994. During 1991–1992, very few adult Colorado squawfish were caught in the lower reach. In 1991, Colorado squawfish 500 mm and longer were captured only in stratum 3 (one fish) and none in strata 1 or 2, resulting in an overall mean CPUE in the lower reach of 0.02 fish (≥500 mm) per net (SE = 0.02; $N = 47$ net sets). In contrast, 42 fish 500 mm or longer were captured with nets in the upper reach, for a mean CPUE of 0.30 (SE = 0.07; $N = 139$). A similar pattern was evident in 1992: Colorado squawfish 500 mm or longer were captured only in stratum 3 (six fish) and none in strata 1 or 2.
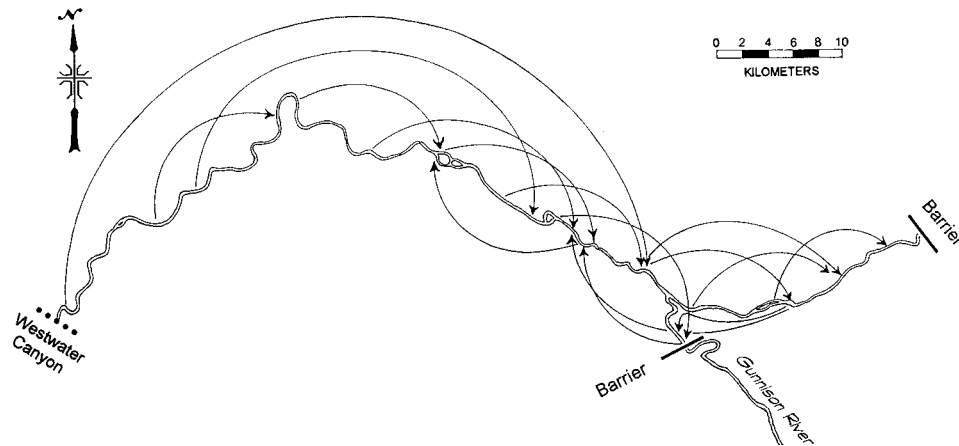
FIGURE 4.—Movement of Colorado squawfish PIT-tagged in the upper reach of the Colorado River. Arrow origins represent capture location; arrow points represent location of next capture. Consecutive captures were at least 1 year apart; only movements greater than 10 km are shown.

Mean CPUE of adults 500 mm and longer was 0.13 (SE = 0.09; N = 49) in the lower reach and 0.46 (SE = 0.09; N = 114) in the upper reach.

By 1993, adult demographics were quite different. Adult Colorado squawfish 500 mm and longer were captured in stratum 1 (17 fish) and stratum 2 (2 fish) for the first time during the study, and CPUE of individuals 500 mm and longer increased to 0.20 per net (SE = 0.04; N = 115 net sets). In the upper reach, 1993 CPUE of adults was 0.57 (SE = 0.10; N = 115). In 1994, catch rates were generally similar to those of 1993 in both reaches. This increase in adult CPUE from 1991 to 1993 coincided with the recruitment of 2–3 strong year-classes produced during the mid-1980s (see Osmundson and Burnham 1998).

Movements

Of Colorado squawfish initially captured and tagged in the upper reach, 69 were recaptured at least once in a subsequent year, and some were recaptured in two or more subsequent years. Including multiple captures of the same fish, there were 92 recaptures during 1991–1995. Of these, 16 (17%) were located farther than 10 km from the previous capture site. Twelve of these 16 displacements were directed upstream (Figure 4), three were directed downstream, and one was directed both downstream and upstream (this fish moved down the Colorado River and up the lower Gunnison River). Of movements entirely within the Colorado River, the portion of displacements directed upstream was higher (test of proportions, P = 0.0098) than predicted if direction was random (50%), though mean distance moved upstream was not significantly different than that moved downstream (P = 0.359). None of the fish captured in the upper reach during the study period was later recaptured in the lower reach.

Of fish initially captured in the lower reach, 37 were recaptured in one or more subsequent years, totaling 43 recaptures during 1992–1995. Of the 43 recaptures, 25 (58%) were located farther than 10 km from the previous capture site. Seventeen (68%) of these long-distance displacements were directed upstream (Figure 5); this proportion was not significantly different than if direction was random (P = 0.086). However, when data from those moving more than 25 km (N = 23) were analyzed, the percent of fish having moved upstream (74%) was significantly different than 50% (P = 0.037). Also, the mean distance of movements (>10 km) directed upstream (108.2 km, SE = 16.5) was significantly greater (t-test, P = 0.0005) than the mean distance of those directed downstream (35.1 km, SE = 6.9).

Many fish captured in the lower reach were later recaptured in the upper reach sometime during the 5-year period: 11 of 25 movements farther than 10 km (44%) were from the lower reach to the upper reach. Though sample sizes were small and sample efforts in 1995 were different from those during 1991–1994, the proportion of fish initially captured in the lower reach and recaptured in the upper reach increased from 1992 through 1995. In 1992, no recaptures of lower-reach fish occurred in the upper reach (0 of 1 recapture); in 1993, 2 of 14 such recaptures (14%) occurred in the upper reach;
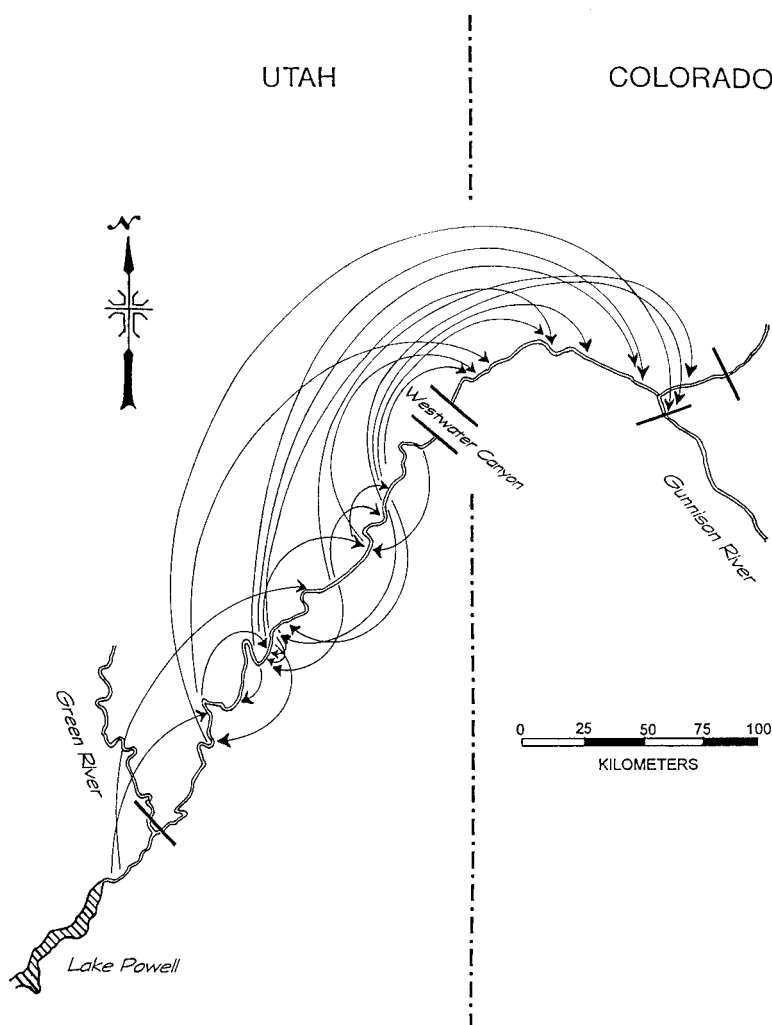
FIGURE 5.—Movement of Colorado squawfish PIT-tagged in the lower reach of the Colorado River. Arrow origins represent capture location; arrow points represent location of next capture. Consecutive captures were at least 1 year apart; only movements greater than 10 km are shown.

TABLE 2.—Total lengths of Colorado squawfish before and after movement from the lower reach to the upper reach of the upper Colorado River. Only those fish moving between reaches based on capture–recapture in consecutive years are included; Rkm = river kilometer location.

Fish number	Lower reach capture			Upper reach capture		
	Year	Rkm	Length (mm)	Year	Rkm	Length (mm)
129	92	81.5	438	93	175.2	478
131	94	96.2	535	95	132.0	580
186	92	98.9	421	93	154.3	449
238	93	58.2	523	94	147.1	539
323	93	26.5	456	94	GU-1.1[a]	466
C-1	94	97.6	555	95	147.5	577

[a] GU = Gunnison River.

in 1994, 5 of 16 (31%) occurred in the upper reach; in 1995, 5 of 12 (42%) occurred in the upper reach.

It was difficult to ascertain a minimum size for Colorado squawfish moving from the lower to the upper reach because recaptures were often 2 years or more apart. Only six lower-to-upper-reach recaptures were 1 year apart. The smallest of these fish was between 421 and 449 mm when it moved; the largest was between 555 and 577 mm (Table 2). For fish with greater recapture intervals, the largest fish was between 570 and 628 mm when it moved to the upper reach sometime during a 2.5-year period.

Distance moved between captures was inversely

TABLE 3.—Length–weight regression coefficients (SEs in parentheses) used in calculation of relative condition of Colorado squawfish captured from the Colorado River during 1990–1994. Relative condition (K_n) was expressed as $K_n = 100 \times M_o/M_e$, where M_o is the observed mass (g) and M_e is the expected mass (g) as calculated from $\log_{10}M_e = \log_{10}(\text{length}) \cdot m + b$. Length is measured in millimeters.

| Month	N	Slope (m)	y-Intercept (b)	R^2
Apr	81	3.17326 (0.061)	−5.54824 (0.167)	0.972
May	257	3.25981 (0.030)	−5.77281 (0.083)	0.978
Jun	128	3.20661 (0.038)	−5.60323 (0.010)	0.983

FIGURE 6.—Mean relative condition (K_n) of Colorado squawfish by length-class and Colorado River reach. Error bars represent 95% confidence intervals.

related to fish size. Mean displacement between consecutive captures was 43.8 km (SE = 15.5; N = 17) for Colorado squawfish less than 500 mm (at time of second capture), 13.3 km (SE = 3.5; N = 68) for fish 500–599 mm (between first and second captures), and 3.1 km (SE = 0.8; N = 34) for fish 600 mm and longer (at first capture). Mean displacement was not significantly different between fish 500–599 mm and those 600 mm and longer, but displacements for both groups were significantly less than for fish smaller than 500 mm (ANOVA, Tukey–Kramer multiple comparison, P < 0.05). Also, mean displacement of fish 550 mm and longer (7.5 km; SE = 2.5; N = 70) was significantly less (t-test, P = 0.008) than that of fish smaller than 550 mm (33.6 km; SE = 10.2; N = 30). The proportion of total displacements consisting of long-distance displacements (>10 km) was significantly different between all size-groups (test of proportions, all P < 0.003) and was inversely related to length: for fish smaller than 500 mm, 59% of displacements were farther than 10 km; for fish 500–599 mm long, 28%; and for fish 600 mm and longer, 6% were long distance.

Body Condition

Mean relative body condition (K_n) of Colorado squawfish varied with river reach and fish length-class (month-specific constants are shown in Table 3). In the lower reach, fish condition declined with increasing length (Figure 6): mean condition factors of fish 500–599 and 600–699 mm were significantly lower (ANOVA, Tukey–Kramer multiple comparison, P < 0.05) than those of fish 200–299, 300–399, or 400–499 mm. Also, mean K_n of fish 400–499 mm was significantly lower than that of fish 300–399 mm (P < 0.05). In contrast, body condition of upper-reach fish increased with fish length, and mean K_n was highest in fish 700–799 mm. Mean K_n of fish 600–699 mm was significantly higher than those of fish 400–499 or 500–
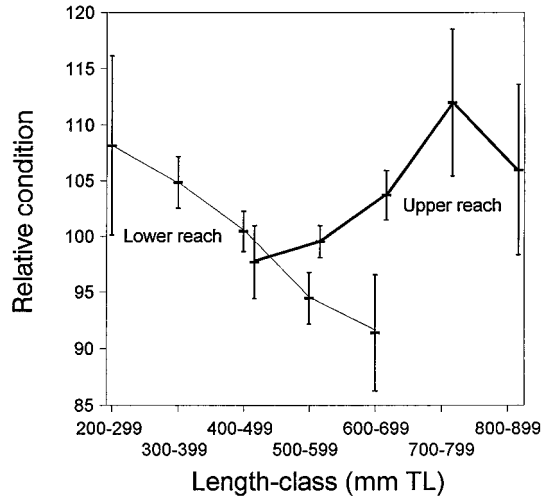
599 mm, and mean K_n of fish 700–799 mm was significantly higher than that of fish 600–699 mm (P < 0.05).

Mean K_n began to differ between reaches once fish attained 500–599 mm. However, reach comparisons could not be made for all length-classes because no fish 200–299 mm and only two 300–399-mm fish were captured in the upper reach, and in the lower reach, no fish 700 mm or larger was captured. Significant differences were detected between reaches within length-classes of 500–599 and 600–699 mm (t-test, P < 0.0004 for both), but not for fish 400–499 mm long (P = 0.14).

Relative Abundance of Forage Fish

Small fish (<100 mm) densities in backwaters were generally higher in the lower reach than in the upper reach: mean annual CPUE (fish per area seined) during fall surveys (1991–1995) was 5.7/m² (SE = 0.4) in the lower reach and 3.3/m² (SE = 0.4) in the upper reach. Results from ANOVA and multiple comparison (obtained by using log-transformed data) indicated that the difference for the 5-year period was significant (ANOVA, P < 0.0000001); however, within years, the only significant difference was in 1994 (Tukey–Kramer multiple comparison, P < 0.05). Three introduced species, red shiner *Cyprinella lutrensis,* fathead minnow *Pimephales promelas,* and sand shiner *Notropis stramineus,* together made up 84–99% of all fish within annual reach samples. Though fish densities within backwaters were lower in the upper

reach, greater backwater area per unit length of river existed there, averaging 0.18 ha/km, than in the lower reach, where backwater area averaged 0.06 ha/km (C. McAda, USFWS, unpublished data). Hence, overall abundance of small forage fish in the two reaches may have been more similar than indicated by CPUE data alone.

Catch rates of larger fusiform, soft-rayed fish were generally higher in the upper reach than in the lower reach, with highest catch rates occurring in the uppermost stratum. Those fish 100 mm and longer included native roundtail chub *Gila robusta,* bluehead suckers *Catostomus discobolus,* flannelmouth suckers *C. latipinnis,* nonnative white suckers *Catostomus commersoni,* and various sucker hybrids. Common nonnative species susceptible to the two gear types but considered largely invulnerable to predation were the deep-bodied common carp *Cyprinus carpio* and the spined channel catfish *Ictalurus punctatus* and black bullhead *Ameiurus melas.*

Electrofishing catch rate of fusiform-shaped fish 100 mm and longer was higher in stratum 3 than in stratum 1 ($P < 0.05$), but CPUE in stratum 3 was not significantly higher than in stratum 2. Catch rates in upper-reach strata were each higher (ANOVA, Tukey–Kramer multiple comparison, $P < 0.05$) than in all lower-reach strata (Figure 7). Among upper-reach strata, the catch rate in stratum 7 was higher than in strata 5 and 6 ($P < 0.05$), and no significant difference was detected between strata 5 and 6. For all fish 100–300 mm (excluding ictalurids), mean electrofishing CPUE was significantly higher in each upper-reach stratum than in any lower-reach stratum ($P < 0.05$), though no differences in CPUE were found among strata within either reach.

Trammel-netting CPUE of fusiform-shaped fish displayed a trend similar to electrofishing with rates generally higher in upstream strata. Catch rates were not significantly different among years within any lower-reach stratum nor among lower-reach strata within years (ANOVA, Tukey–Kramer multiple comparison, $P > 0.05$). The CPUE in stratum 5 was significantly higher ($P < 0.05$) than that in stratum 1 during 1992 and 1994 and higher than stratum 3 CPUE in 1994. In stratum 6, CPUE was significantly higher than in stratum 1 in all years, higher than in stratum 3 in 1993 and 1994, and higher than in stratum 5 in 1993. In stratum 7, CPUE was significantly higher than in all other strata except stratum 6 in 1993. When all three years were considered, CPUE in stratum 7 was
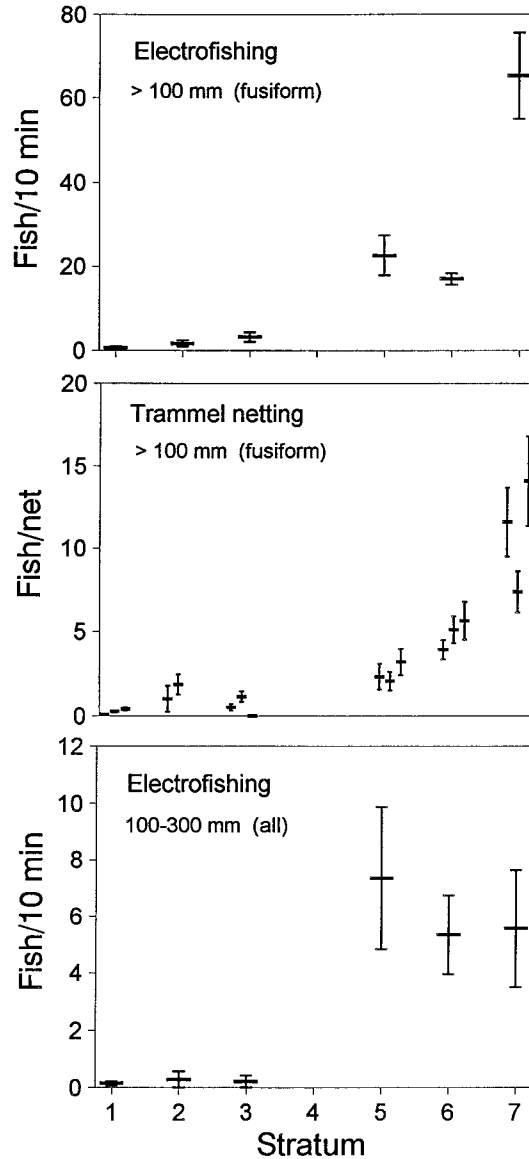

FIGURE 7.—Electrofishing and trammel-netting catch per unit effort (CPUE) by stratum for potential forage fishes of large Colorado squawfish. Electrofishing (top) and trammel netting (middle) catches of fusiform fish more than 100 mm in total length include roundtail chub, flannelmouth sucker, bluehead sucker, white sucker, and sucker hybrids. Electrofishing CPUE of fish 100–300 mm (bottom) includes all species except channel catfish and black bullhead. For trammel netting, separate bars within each stratum represent CPUE from (left to right) 1992, 1993, and 1994 (no 1994 data in stratum 2); electrofishing was conducted in 1993 only. Vertical lines are ±SE of the geometric mean.

TABLE 4.—Diets of Colorado squawfish (400–550 mm total length) during spring 1994. Values are overall volumes of each food item as a percentage of total volume (100%) and are averages from all fish containing food (see text); UI = unidentified; MOD = miscellaneous organic debris.

Component	Reach		Habitat	
	Lower (N = 16)	Upper (N = 17)	Back-waters (N = 30)	Channel (N = 9)
UI fish parts	23.6	35.8	30.2	20.8
UI fish	24.5	2.9	11.5	11.5
Fathead minnow	27.2	28.2	35.3	27.6
Red shiner	0.0	11.1	6.8	0.0
Sand shiner	13.7	0.0	1.3	25.1
Roundtail chub	9.3	0.0	3.3	5.8
Green sunfish				
Lepomis cyanellus	0.0	5.8	3.3	0.0
White sucker	0.0	10.9	6.2	0.0
Annelids	0.9	0.7	1.0	0.7
MOD	0.8	4.5	1.0	8.6

significantly higher than in all other strata, and stratum 6 CPUE was higher than that in stratum 5.

Diet

The modified Seaburg stomach sampler proved effective in removing stomach contents from Colorado squawfish smaller than about 550 mm. For larger adults, the method was abandoned due to persistent difficulties associated with (1) handling the fish while attempting to manipulate the flushing tube, (2) passing tubes of sufficient length and diameter (to encapsulate large prey) down the esophagus, and (3) producing sufficient flushing pressure with the squeeze bulb for forcing items through the large tubes. Efforts to encourage large fish to regurgitate their stomach contents by using tartar emetic (after Jernejcic 1969) were also abandoned because of apparent stress to the fish.

Diets of Colorado squawfish 400–550 mm captured in the upper reach were similar to those of fish captured in the lower reach and were similar between fish captured from main channel and backwater habitats (Table 4). Fish in stomach samples were generally small: lengths of fathead minnows, the most common prey, averaged 51 mm (SL) whereas roundtail chub and white sucker averaged 85 and 70 mm (SL), respectively. Of stomachs containing identifiable fish ($N = 27$), 63% contained one fish; 26% contained two or three fish; 4% contained five fish; and 7% contained six or seven fish. Feeding rate may be reduced in this species prior to spawning: significantly more (test of proportions, $P = 0.002$) sampled fish 400–550 mm (TL) had empty stomachs from 26 May to 20 June (93%, $N = 14$) than fish sampled before 26 May (41%, $N = 58$) in the early spawning year of 1994. Percentages of empty stomachs before 26 May were similar ($P > 0.05$) between lower (38%, $N = 26$) and upper reaches (44%, $N = 32$).

Temperature

Annual thermal units for growth decreased in an upstream direction as expected (Table 5). As a percentage of thermal units in stratum 1, thermal units in stratum 3 were 93%; in stratum 5, 81%, in stratum 6, 71%; in stratum 7, 62%; at Cameo, 54%; and at Rulison, 42%. Thermal units decreased between sites in strata 1 and 3 by an average of 0.08 units/rkm; between strata 3 and 5 sites by 0.17/rkm; between strata 5 and 6 sites by 0.15/rkm; between strata 6 and 7 sites by 0.23/rkm; between stratum 7 and Cameo sites by 0.24/

TABLE 5.—Total annual thermal units for Colorado squawfish growth at seven temperature-monitoring stations along the Colorado River. Bold italics indicate missing values that were estimated. Missing values for stratum 1 were estimated by using the relationship between thermal growth units there and at the stratum 3 or stratum 5 sites; missing values for strata 3 and 6 were estimated from stratum 5 values; missing values for the Rulison (R) site were estimated from the Cameo (C) site values. No thermograph was located in stratum 7 during the 1992–1996 period; all yearly totals are estimates based on the relationship between thermal growth units there and at the Cameo site (a ratio of 1.165:1) developed during 1986–1991 (not shown); Rkm = river kilometers upstream of the confluence with the Green River.

Location		Year					
Stratum or site	Rkm	1992	1993	1994	1995	1996	Mean (SE)
1	87.4	100.9	68.3	97.6	*53.1*	85.2	81.0 (9.0)
3	158.2	*85.3*	*53.5*	96.7	47.2	77.2	72.0 (7.5)
5	214.6	73.6	46.2	87.4	39.2	65.9	62.5 (7.5)
6	264.7	*63.9*	41.3	75.9	34.6	59.4	55.0 (8.8)
7	292.8	*60.4*	*34.0*	*68.8*	*29.7*	*49.3*	48.4 (9.4)
C	321.4	51.9	29.2	59.1	25.5	42.3	41.6 (6.4)
R	369.9	*40.4*	*22.8*	46.6	19.1	33.8	32.5 (5.2)

rkm; and between Cameo and Rulison sites by 0.19/rkm.

Discussion

This study coincided with the recruitment of two or three consecutive strong year-classes to the adult Colorado squawfish population. This allowed us to monitor the movements of many individual fish and observe changes in adult distribution resulting from these year-classes. Dispersal was generally in an upstream direction, but recruitment also increased adult abundance riverwide. Mean lengths increased in the lower reach as young fish grew, and the influx of young adults moving to the upper reach from the lower reach reduced average sizes of fish in the upper reach.

Distance moved between captures was related to fish size and reach of initial capture. Most fish initially captured in the upper reach moved little from initial capture sites and were predominately larger adults. However, most fish initially captured in the lower reach were smaller individuals and were often recaptured farther than 10 km from initial capture sites. In both reaches the majority of movements were directed upstream. These movement patterns suggest that young fish move more than older fish, and less movement occurs after arrival in the upper reach. Flannelmouth suckers in the White River behaved in a similar way with young individuals having moved more than older ones (Chart and Bergersen 1992).

Movement to upstream strata by adults suggests that upper reach habitats are preferred or have a better mix of requisites for growth and survival. Particularly revealing was the lack of fish movements from the upper reach to the lower reach. Riverwide catch rate patterns of larger prey species combined with reach differences in Colorado squawfish body condition support the hypothesis that upstream displacements are a response to food resource gradients.

Relatively small changes in location by larger fish in the upper reach was consistent with the hypothesis that adult Colorado squawfish select and maintain fidelity to a home feeding range, as suggested by Tyus (1990), McAda and Kaeding (1991), and Ryden and Ahlm (1996). Adults of this species appear not to be highly territorial (as defined by Hixon 1980) given that they concentrate in limited backwater habitats during spring runoff (April–June), they congregate prior to and during spawning in summer (Tyus 1990), and individuals are occasionally located (via radiotelemetry) be-side one another (USFWS, unpublished data) during base flows of fall and winter.

High relative condition of Colorado squawfish 200–399 mm in the lower reach suggests that food for young Colorado squawfish was not limited (at least during spring), and may relate to the high numbers of small-bodied, nonnative minnows in backwaters there. However, relative condition declined in the lower reach as Colorado squawfish grew, suggesting that a diet consisting of small minnows may be insufficient for larger individuals. If so, the lack of appropriate-sized prey may be particularly acute in the lower reach where warmer temperatures increase metabolic demands. Although little is known of food habits of larger adult Colorado squawfish (and we were unsuccessful in collecting such data), anecdotal evidence indicates consumption of larger prey than was found for size-classes examined in this study. A 687-mm Colorado squawfish captured in the San Juan River regurgitated a flannelmouth sucker 235 mm long—34% of its own length (D. Propst, New Mexico Department of Game and Fish, personal communication). One 860-mm individual that we captured in the lower Gunnison River regurgitated a 310-mm white sucker × bluehead sucker hybrid (36% of its length). An X-rayed, 599-mm adult from the White River contained a 280-mm (47% of its length) unidentified sucker (J. Hawkins, LFL, personal communication). Scott and Crossman (1973) reported the optimum food size of northern pike was one-third to one-half the pike's length and that growth and survival of large muskellunge are often impaired if food of an adequate size is not available, despite vast numbers of smaller fishes. Gillen et al. (1981) similarly reported an optimum prey size for tiger muskellunge *E. lucius* × *E. masquinongy* as 40% of total predator length when prey were soft-rayed and fusiform shaped. Also, of three simulated mechanisms, lack of large prey had the strongest effect on stunting of northern pike (Diana 1987).

The most downstream thermograph site provided the most days with temperatures at or near 25°C, the preferred temperature of yearling (Black and Bulkley 1985a) and adult Colorado squawfish (Bulkley et al. 1981), and the greatest number of annual thermal units for growth. In addition, main-channel temperatures there never became too warm for these fish: daily averages never exceeded 26°C during 4 years of monitoring. Therefore, growth potential should be highest in the lower reach. However, warm water temperatures there may be disadvantageous for adults: higher meta-

bolic demands require more food, but appropriate food for adults is scarce.

Evidently the motivation for upstream dispersal is strong given that these movements are against the current and away from a more preferred thermal regime. Stuntz and Magnuson (1976) reported that preferred temperatures of bluegills *Lepomis macrochirus* decreased in laboratory studies as food ration decreased, and they suggested that bluegills use temperature selection as a method of decreasing weight loss during periods when daily rations are low. We suggest here that this same phenomenon, acting in concert with searches for greater food availability, motivate upstream dispersal in Colorado squawfish and result in the longitudinal structuring of size distributions observed in the Colorado River.

Factors other than changing food requirements may induce long-range displacements by adult Colorado squawfish; these include predator avoidance, reproduction, and physical habitat preferences. Of these, predator avoidance is probably least important given the rarity of predators capable of preying on adult Colorado squawfish. Because seasonal movements related to spawning were excluded from our analyses, displacements from one spring period to the next were probably not the direct result of reproductive behavior; that is, Colorado squawfish generally return to non-spawning home ranges by late summer or fall (Tyus 1990; McAda and Kaeding 1991). Searches for areas containing preferred meso- or microhabitats may contribute to observed movements and distribution, particularly within strata. However, because habitat and food are so tightly interrelated, it is difficult to separate selection for food from selection for habitat types that allow efficient foraging (Magnuson et al. 1979). It seems reasonable to assume that in an environment with minimal intraspecific competition and predation risk, positioning of adults, both within and among strata, would be primarily driven by growth maximization (see Hughes 1998), and growth is largely dependent on the interaction of temperature and food availability (Weatherley 1972). Achieving maximum growth potential enhances the ability of the individual to survive and reproduce successfully. In many fish species, large females produce more and larger eggs, thereby enhancing larval survival (Monteleone and Houde 1990; Brandt and Kirsch 1993).

Adults probably select reaches containing the best combination of resources, and the upper reach, particularly strata 6 and 7 (the Grand Valley)

where adults were most concentrated, may represent the best balance between suitable temperatures and food availability. At some distance upstream, annual thermal units should decline to the point where plentiful forage can no longer provide adequate compensation, resulting in reduced growth. This probably occurs within the reach immediately upstream of the Grand Valley where annual thermal units are low. At Rulison, mean daily temperatures never reached 20°C during 3 of the 5 years studied. Black and Bulkley (1985b) found that growth of yearling Colorado squawfish held at 20°C and fed unlimited food was only 54% that of growth at the optimum temperature of 25°C. This reach, blocked by diversion structures since the turn of the century, may represent the fringe of the former range of this species in the Colorado River.

Seasonal timing of and stimulus for movement could not be discerned in this study by comparing consecutive capture events. However, the available evidence allows us to offer four hypotheses. First, movements may be motivated by hunger with upstream exploration for food being more rewarding than downstream exploration. Second, an innate physiological mechanism may prompt upstream movement; however, the lack of dispersal movements in many fish and the downstream movement of some are counter to a species-wide directional disposition. Third, movements may be motivated by the urge to spawn, and better feeding areas are discovered in the process. Movement primarily by sexually mature individuals supports the latter hypothesis, but sizable numbers of adult fish are found in upper White and Yampa river reaches far upstream of their spawning areas (Tyus 1990), suggesting that upstream feeding areas were not located while en route to a spawning site.

A fourth hypothesis, combining the hunger and spawning hypotheses above, may be the most plausible given all lines of circumstantial evidence. Gradients in food resources may be discovered by young adults during their initial spawning migrations, and these learned gradients are then pursued after the spawning period is completed, resulting in further upstream explorations by young adults. If this latter hypothesis has merit, we might predict that such displacements take place during and immediately following the spawning period.

The extent to which distribution and dispersal patterns observed in this study reflect historic conditions is unknown. Intraspecific competition formerly might have played a role in structuring riverwide size distributions; now such competition in

the upper reach is probably low given the relative rarity of these endangered fish. Also, nursery areas might not have been exclusively located in the lower reach as is largely the case today: data from the mid-1970s indicate that small size-classes of Colorado squawfish were much more abundant in the upper reach (see Osmundson and Burnham 1998). Predation from introduced largemouth bass *Micropterus salmoides* and green sunfish *Lepomis cyanellus,* now commonly found in upper-reach backwaters, may partly explain the current lack of young Colorado squawfish there. Also, prey of large Colorado squawfish (native suckers and chubs) may have once been more abundant in the lower reach than is the case today. The overall pattern observed in this study (i.e., large fish upstream; younger fish downstream), makes sense as a life history strategy and may partially reflect an adaptation to modified riverine conditions. The lower reach provides warmer water and ample food for early life phases when rapid growth is most important for survival; the upper reach provides moderated temperatures and more appropriately sized prey for adults when maintaining body condition may be important in gamete production and in fueling spawning migrations.

Long-distance dispersal is a manifestation of the individual's solution to spatial and temporal problems (Baker 1982), and exploratory movements across considerable distances are probably searches for suitable habitats (McKeown 1984). The distribution and dispersal patterns of Colorado squawfish in the Colorado River indicate that dispersal movements of this species occur at the landscape scale, and large sections of river are required to meet the changing needs of different life stages.

Acknowledgments

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