THE SOUTHWESTERN NATURALIST 41(2):161–168 JUNE 1996

OBSERVATIONS ON THE DISTRIBUTION AND MOVEMENTS OF COLORADO SQUAWFISH, *PTYCHOCHEILUS LUCIUS*, IN THE SAN JUAN RIVER, NEW MEXICO, COLORADO, AND UTAH

DALE W. RYDEN AND LIEF A. AHLM

United States Fish and Wildlife Service, Colorado River Fishery Project, 764 Horizon Drive, South Annex A, Grand Junction, CO 81506-3946 (DWR)
New Mexico Department of Game and Fish, County Road 4225, #8, Navajo Dam, NM 87419 (LAA)
Present address of LAA: New Mexico Department of Game and Fish, P.O. Box 360, Chama, New Mexico 87520

ABSTRACT—Seventeen adult Colorado squawfish (*Ptychocheilus lucius*) were captured between June 1991 and October 1994 during sampling conducted on the San Juan River in New Mexico, Colorado, and Utah. Thirteen individuals were surgically implanted with internal radio transmitters. Telemetry, capture, and recapture data indicated that most adult Colorado squawfish were sedentary and had a strong affinity for a 39.0 km reach of the river (river km 228.2 to 189.2) upstream of the Colorado-Utah border. Seven fish aggregated prior to spawning in and around the Mancos River confluence (km 197.3). Eleven fish, including six of the seven that aggregated in the vicinity of the Mancos River, moved a short distance upstream to a 5.8 km reach of the river (km 214.6 to 208.8) during the probable spawning seasons (late June to mid-August). Only one radiotelemetered Colorado squawfish during our study displayed migratory behavior and then only in association with spawning. Life stages of Colorado squawfish were spatially separated, with adults generally occurring upstream of captured larvae and juvenile fish. The recent formation of a waterfall at the confluence of the San Juan River and Lake Powell, and its subsequent inundation, poses a management conundrum for all life stages of this endangered species in the San Juan River. The waterfall appears to be a physical barrier to the upstream movement of adult Colorado squawfish from Lake Powell. However, it also seems to inhibit the invasion of the lower San Juan River by lentic predators, thereby protecting early life stages of Colorado squawfish that are found almost exclusively in this section of the river.

Colorado squawfish, *Ptychocheilus lucius*, formerly occupied the mainstem Colorado River, its major tributaries, and the Colorado River delta in Mexico (Jordan and Evermann, 1896). Once abundant enough to be pitch-forked from irrigation canals in central Arizona (Miller, 1961), natural populations were extirpated from the Lower Colorado River Basin (Minckley, 1973) and greatly reduced in the Upper Basin by the late 1960's (Holden and Wick, 1982; Tyus et al., 1982; U.S. Fish and Wildlife Service, 1990). Herein, the Upper Colorado River Basin refers to the Colorado River drainage upstream of Lee's Ferry, Arizona, with the Lower Basin being downstream of that point. Colorado squawfish currently occupy about 20% of their historic range (Tyus, 1990). The largest surviving populations of the species occur in the Green, White, Yampa, and Colorado rivers above Lake Powell (Holden and Wick, 1982; Tyus, 1991). The San Juan River supports a small, but reproducing population of Colorado squawfish (Minckley and Carothers, 1979; Platania et al., 1991). Large-scale water development, introduction and establishment of non-native fish species, and habitat degradation along the river corridor, as well as other factors have contributed to the decline of the species (summarized in Wydoski and Hamill, 1991). Its reduced distribution and abundance prompted its federal listing as endangered (United States Department of the Interior, 1974). It is also protected under state law in the Upper Basin states of Colorado, New Mexico, and Utah.

Research on Upper Basin Colorado squawfish populations (Tyus and McAda, 1984; Tyus, 1990; McAda and Kaeding, 1991) indicates that populations tend to be made up of two types of individuals, those that are sedentary and others that

are highly vagile. Sedentary behavior in Colorado squawfish has been linked to sexual immaturity, non-annual spawning, or adult fish that spawn in the same area in which they reside (Tyus, 1990). Sexual immaturity or non-annual spawning may result in an individual fish displaying sedentary behavior during part of its life cycle and subsequent migratory behavior during other periods.

Telemetry studies on Colorado squawfish in the Green and Yampa rivers found that most sexually mature fish make long spawning migrations to a few, specific areas of each river (Tyus et al., 1981; Tyus, 1986, 1990). However, a separate study on the Colorado River did not detect long distance spawning migrations or spawning congregations of radiotelemetered fish (McAda and Kaeding, 1991). This was attributed to widespread occurrence of suitable spawning habitat in the Colorado River, thereby eliminating the need for long migrations. Although differences in spawning movements were reported among these rivers, adult Colorado squawfish in each usually returned to an autumn to spring home range after the spawning season (Tyus, 1990; McAda and Kaeding, 1991).

The San Juan River, the southern-most, Upper Basin tributary to the Colorado River, originates in the San Juan Mountains of southern Colorado and drains portions of Colorado, New Mexico, Arizona, and Utah before entering Lake Powell in Southeastern Utah. This river is bound by large reservoirs at either end, and with the exception of the Animas River near Farmington, New Mexico is fed only seasonally by small tributaries. One such tributary, the Mancos River enters the San Juan River in Colorado just upstream of the Four Corners area (km 197.3). This small, shallow tributary usually has peak runoff that precedes that of the San Juan River and is warmer in temperature that the San Juan during the spring and early summer. By late summer the Mancos River is often dry.

As a result of the construction of Navajo Reservoir above Farmington, New Mexico in the early 1960s and its hypolimnetic release, only about 288 km of the San Juan River upstream of Lake Powell currently provide habitat for Colorado squawfish (Holden and Wick, 1982; Bestgen and Williams, 1994).

Broad-based, multi-agency and multi-disciplinary studies on Colorado squawfish and other native fishes of the San Juan River were initiated in 1991. The objective of these studies were 1) to inventory populations of native fish in the San Juan River; 2) identify their habitat needs; 3) identify factors contributing to the endangered status of the Colorado squawfish and razorback sucker (*Xyrauchen texanus*); and 4) monitor responses of native fish populations to test flows from Navajo Reservoir. Herein we report on one aspect of this research; the distribution and movement patterns of adult Colorado squawfish.

MATERIALS AND METHODS—From 1991 through 1994, 14 sampling trips were conducted along the 288 km section of river from Farmington, New Mexico to Clay Hills Landing, Utah, just above Lake Powell (Fig. 1). Sampling occurred in May and October of each year, with additional efforts in June 1991 and 1992, April and July 1993, and April and August 1994. Raft-borne electrofishing units (5000 Watt generator-powered with variable voltage and amperage, direct current output) were used to stun adult fish along shoreline habitats. Stunned fish were captured with dip nets and held in live wells for processing. Trammel nets (1-in. inside panel mesh, 10-in. outside panel mesh) were used in backwaters, side channels, and mouths of seasonally watered tributaries.

Following capture, all adult Colorado squawfish were anesthetized with 200 mg/l (Tyus and McAda, 1984) of tricaine methanesulfonate (MS-222), weighed (±5 g), measured in mm total length (TL), tagged with Passive Integrated Transponder (PIT) tags, and had tissue plugs taken for genetic analysis. Thirteen adult Colorado squawfish were surgically implanted with 40 khz radio tags (battery lives 9, 12, or 24 months), and released. Expired, or nearly expired, radio tags were removed from four recaptured fish and each fish was reimplanted with a new tag. Radio-tagged fish were released as near their capture location as possible, within 0.5 h of capture.

Tracking was conducted year-round, but was more intensive during presumed pre-spawning and spawning periods (weekly) than during the remainder of the year (every second week or monthly). Tracking consisted of both ground and aerial contacts. Ground contacts were triangulated to ±5 ft. using a hand-held directional antenna. Aerial contacts were determined to the nearest 0.1 mi. Telemetry data were analyzed to characterize general movement patterns and to locate possible spawning habitat. Contacts were classified by time of year (pre-spawn: mid-May to beginning of spawning season; spawning season; and rest of the year), and location (Mancos: km 197.3; Mixer: km 214.6 to 208.8; and elsewhere in the river). The presumed spawning season was based on the maintenance of a daily mean, main-channel water temperature of 18°C or greater in the river reach between Shiprock, New Mexico (km 238.0) and the Four Corners Bridge

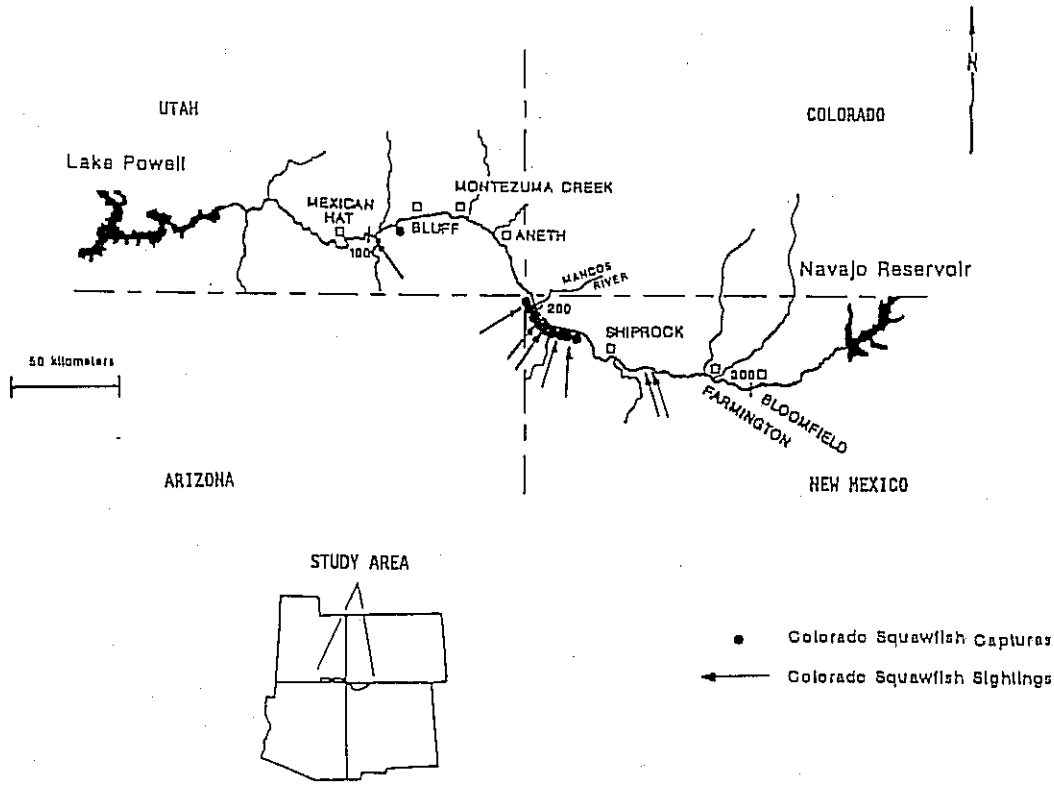

FIG. 1—San Juan River study area showing locations of Colorado squawfish captures and observations, 1991 to 1994. Dots (offset from the river) indicate capture locations and arrows indicate observations of adult Colorado squawfish. Numerals indicate river kilometers.

near the New Mexico-Colorado-Utah-Arizona borders (km 191.8). This temperature is a baseline threshold at which Colorado squawfish begin to exhibit spawning behavior (Hamman, 1981; Nesler et al., 1988; McAda and Kaeding, 1991).

Distance between the most upstream contact and the most downstream contact (total longitudinal movement), maximum distance and direction moved from point of release (maximum displacement), and distance and direction from point of release to point of last contact (final displacement) were calculated for each fish. Fish were categorized as displaying either sedentary or migratory behavior based on total movement. Sedentary behavior was defined as making only localized movements (i.e., total longitudinal movement $\leq$35 km), while migratory behavior entails total longitudinal movements of >35 km (Tyus, 1990).

RESULTS—Seventeen adult Colorado squawfish were captured between June 1991 and October 1994. They ranged in size from 521 to 948 mm TL and from 1.2 to 8.0 kg. Eleven of these fish were females and six were males. Four of these fish were also recaptured for a total of 21 captures.

Colorado squawfish were captured between km 228.2 and km 120.4 (Fig. 1). Sixteen were captured in a 36.7 km reach of the San Juan River between Cudei Diversion (km 228.5) and the Four Corners Bridge (km 191.8). Five additional Colorado squawfish were sighted, but not captured in this river reach. Three of four recaptures were also in this reach. The remaining Colorado squawfish was captured near Bluff, Utah (km 120.4) in October 1993 and recaptured in the same area in May 1994. A single Colorado squawfish sighting occurred in the main channel at km 105.5 in May of 1995. Of the 21 captures, 4 occurred in April (3 females, 1 male), 3 in May (2 female, 1 male), 5 in June (2 females, 3 males), and 9 in October (8 females, 1 male).

Thirteen fish (8 females, 5 males) were implanted with radio transmitters. A total of 220

TABLE 1—Total longitudinal movement (TLM), maximum displacement (MD), and final displacement (FD) of radiotelemetered Colorado squawfish in the San Juan River, New Mexico and Utah, 1991 to 1994.

Fish Number	Release km	Number of contacts (air & ground)	Number of days between capture and last contact	TLM in km	MD in km	FD in km
1	217.1	12	227	7.2	4.9 (−)[1]	1.8 (−)
2	197.3	20	369	27.7	22.2 (+)	2.1 (−)
3	197.3	13	340	14.2	14.2 (+)	5.0 (+)
4	205.2	18	312	24.0	16.1 (+)	7.8 (+)
5	204.3	12	266	14.8	7.7 (+)	3.5 (+)
6	202.3	20	356	15.1	10.1 (+)	2.9 (−)
7	209.3	36	513	16.9	15.5 (−)	15.5 (−)
8	209.3	10	166	1.8	1.8 (+)	0.3 (+)
9	222.0	5	140	32.8	32.8 (−)	32.7 (−)
10	206.9	25	538	21.2	21.2 (+)	11.6 (+)
11	196.2	21	509	18.0	16.0 (+)	12.3 (+)
12	120.2	16	416	93.0	91.2 (+)	0.3 (+)
13	214.0	12	172	18.8	17.9 (−)	0.8 (+)
Mean				23.5	20.9	7.4
Standard Error				6.2	6.3	2.5

[1] (+) represents upstream movement, (−) represents downstream movement. All numbers are positive values.

contacts with radio-tagged fish was made during 20 ground and 48 aerial trips between June 1991 and October 1994. All radiotelemetered Colorado squawfish (n = 12) that were captured in New Mexico displayed sedentary behavior (mean total longitudinal movement [TLM] = 17.7 km, SE = 2.4; mean maximum displacement [MD] = 15.0 km, SE = 2.4), remaining in a 39 km reach of river (km 228.2 to 189.2) throughout their respective tracking periods (Table 1). As a group, radiotelemetered Colorado squawfish tracked during our study (n = 13) moved only short distances (mean TLM = 23.5 km, SE = 6.2). Small values were also obtained for MD (mean = 20.9, SE = 6.3) and final displacement (mean = 7.4, SE = 2.5). The individual captured in Utah was the only fish that displayed migratory behavior. After remaining within 3.7 km of its initial capture location for 8 months, it moved 93.0 km upstream in less than a month. It remained in the spawning area for slightly less than two months, then moved downriver, and was contacted 0.6 km from its initial capture location 10 days after departing the spawning area (Table 1).

Forty-nine contacts were made with radiotelemetered Colorado squawfish during pre-spawning periods from 1991 through 1994. Seven radiotelemetered Colorado squawfish, five females and two males, aggregated during pre-spawning periods in or near the mouth of the Mancos River, prior to moving to presumed spawning bars (Table 2). Two fish in each of the first three years, and three fish in 1994 exhibited this behavior. Two of the seven (fish numbers 2 and 11, Table 2) were females that aggregated at the Mancos in more than 1 year and subsequently moved to the presumed spawning areas. These seven fish accounted for 21 (42.9%) of 49 contacts with Colorado squawfish during pre-spawning periods. Nineteen contacts occurred elsewhere in the river, and nine contacts occurred in the Mixer during pre-spawning periods. Eight of the contacts elsewhere in the river were with five of the seven fish that aggregated in the Mancos River. Their contact locations ranged from 3.1 km below to 5.0 km above the Mancos River. Another large female (687 mm TL), gravid and emitting eggs, was captured at the mouth of the Mancos River in a trammel net on 9 June 1991 with two other Colorado squawfish (one female and one male, both radio-tagged). This female was not radio-tagged.

Of the remaining six radiotelemetered fish, only four had active radio tags during pre-spawning periods. These four fish accounted for 11 of the 19 contacts elsewhere in the river and all nine radio contacts within the Mixer reach during pre-spawning periods. Three of these remained up-

TABLE 2—River used and movement patterns of radiotelemetered Colorado squawfish in the San Juan River 1991–1994.

Fish Number	Sex	Total length at last capture (mm)	River used[1]	Contacted in mixer during spawning	Movement pattern
1	M	571	S	yes	sedentary
2	F	754	M (×2)[2]/S	yes	sedentary
3	M	610	M/S	yes	sedentary
4	F	630	M/S	yes	sedentary
5	F	948	M/S	yes	sedentary
6	F	647	M/S	yes	sedentary
7	M	521	S	yes (×2)	sedentary
8	M	595	S	yes	sedentary
9	F	705	S	no	sedentary
10	F	820	S	yes	sedentary
11	F	764	M (×2)/S	yes (×2)	sedentary
12	F	762	S	yes	migratory
13	M	617	M/S	no	sedentary

[1] S = San Juan River, M = Mancos River.
[2] (×2) = A fished used this area during two separate pre-spawn or spawning seasons.

stream of the Mancos River and the fourth was located downstream near Bluff, Utah. The Bluff fish moved upstream past the Mancos to the presumed spawning area and was not documented in the vicinity of the Mancos River confluence.

Thus, of 11 individuals with active tags during pre-spawning periods, seven (63.6%) used the Mancos River confluence area during that time of the year. Including the large, gravid female captured there, eight (47%) of the 17 captured Colorado squawfish are known to have used the Mancos River confluence area during pre-spawning periods. No radio-tagged fish were found near the Mancos River confluence at any other time of the year.

Between 1991 and 1994, 11 (84.6%) of 13 radiotelemetered Colorado squawfish, including six of seven that aggregated at the Mancos River, moved to the Mixer (km 214.6 to 208.8) during spawning periods. Seven were female and four were male. One male was ripe, tuberculate, and releasing milt when captured on 28 June 1992 and was later located near a suspected spawning bar within several meters, based on ground triangulation, of a female Colorado squawfish (10 July 1992). Two individuals (one male, one female) were contacted in the Mixer in two consecutive years (Table 2). Of 72 radio contacts made with Colorado squawfish during presumed spawning periods, 50 (69.4%) occurred in the Mixer. Fifteen of the remaining 22 contacts were with fish that spent part, but not all of their time in the Mixer during a given spawning season. The other seven contacts were split between a female fish (fish number 10, Table 2) that used the Mixer during the second of two spawning seasons in which she was tracked (three contacts), and a male (fish number 13, Table 2) that utilized the Mancos River, but did not move upstream to the Mixer during the spawning period.

During the rest of the year, radiotelemetered Colorado squawfish were spatially separated from one another, with some being upstream and some downstream of the presumed spawning areas.

DISCUSSION—The majority of Colorado squawfish captured and radio-tracked during our study (1991 through 1994) utilized a short section (km 228.2 to 189.2) of the San Juan River. Given the relatively large percentage of contacts, 209 (95.0%) of 220, with Colorado squawfish in this 39.0 km reach and the dearth of adult fish collected or observed elsewhere in the river, it appears that this reach has undefined qualities or characteristics that make it a "preferred" reach. The five Colorado squawfish that were sighted, but not captured in this river reach, lend further credence to the importance of this area. Six of eight Colorado squawfish captures and one of two sightings in a 1987 to 1989 study (Platania et al., 1991) were also in or very near (km 234 to 186) this same section of river.

Radiotelemetered Colorado squawfish tracked during our study moved only short distances despite being large, sexually mature fish (Tyus and McAda, 1984). The small values obtained for total longitudinal movement and final displacement indicated that the majority of San Juan River Colorado squawfish are sedentary in that they have a small home range, within which spawning evidently occurs. However, a small number of Colorado squawfish in the San Juan are migratory, as evidenced by the one fish in this study that moved 93 km. In addition, a Colorado squawfish captured and tagged in Lake Powell in April 1987 (615 mm TL) was recaptured in September 1987 (632 mm TL), 127 km upstream near Bluff, Utah (Platania et al., 1991).

A portion of the San Juan River Colorado squawfish population aggregated in and around the Mancos River confluence (km 197.3) in May and early June and then moved a short distance to the Mixer (km 214.6 to 208.8) presumably for spawning. Physical habitat studies verified that suitable spawning habitat existed within the Mixer (R. Bliesner and V. Lamarra, pers. comm.). Two of five individual Colorado squawfish tracked in multiple years aggregated at the Mancos River during two separate pre-spawning periods. One of these fish (as well as another of the five individuals) used the Mixer during two separate spawning seasons. This indicated a seasonally repeated behavior, probably associated with spawning (Tyus and McAda, 1984).

Currently, the Mancos and Mixer are the only known pre-spawn gathering and probable spawning areas for Colorado squawfish in the San Juan River. However, not all San Juan River Colorado squawfish appeared to aggregate or spawn every year, at least not at these locations. One large female tracked in two consecutive years was not contacted in the Mancos and moved to the Mixer during only one spawning season. In addition, a small male contacted in and near the Mancos River in 1994 did not move to the Mixer during that spawning season. Other pre-spawn gathering and spawning areas may exist in the San Juan River that have not been located. Captures and observations in the San Juan River near Bluff, Utah, both during this study (one capture and one observation), and in the 1987–1989 study (one capture and one observation; Platania et al., 1991) suggest that a group of Colorado squawfish may reside there. However, the availability of suitable spawning habitat in this section of the San Juan River is unknown.

Capture of early life stages of Colorado squawfish downstream from the presumed spawning area substantiates successful reproduction in the San Juan River in 1993 and 1994 (M. Buntjer et al., in litt.; K. Lashmett, in litt.). Larval fish were distributed downstream in a pattern similar to that reported for other Upper Basin rivers (Tyus, 1986). All larval and juvenile Colorado squawfish, including those collected in the 1987 to 1989 study (Platania et al., 1991), were collected downstream of the presumed spawning site within the Mixer reach, being distributed from just above the Mancos River to Lake Powell. Most of these were collected below Montezuma Creek (km 148.3). It is not known if these early life stage fish were progeny of fish spawning in the Mixer or elsewhere.

San Juan River Colorado squawfish display many of the characteristics of other Upper Basin Colorado squawfish populations, but are unique in other aspects. The pattern of a pre-spawn aggregation of Colorado squawfish at the mouth of a tributary (the Mancos River) before moving to a known or probable spawning area has not been apparent in other Upper Basin rivers. In the Green and Yampa Rivers, adult Colorado squawfish make repeated long distance migrations to a few known spawning areas (Tyus et al., 1981; Tyus, 1986, 1990), much like the seasonally repeated movement of San Juan River fish to the Mixer reach. However, unlike Green and Yampa River fish, the majority of San Juan River Colorado squawfish do not move long distances but reside in the area in which they spawn, as do Colorado River populations of Colorado squawfish, (McAda and Kaeding, 1991). Small values obtained during our study for final displacement (mean = 7.4 km, SD = 2.5) suggest that, after the spawning season, San Juan River Colorado squawfish, including the single migratory fish in our study, return to a small home range. This behavior was also noted in Upper Basin Colorado squawfish (Wick et al., 1983; Tyus, 1985; McAda and Kaeding, 1991).

Throughout most of the 1980s Lake Powell was filled to capacity, inundating the lower 22.5 km of the San Juan River. This enabled species such as the Colorado squawfish to travel freely from riverine habitats to Lake Powell and back, as is evidenced by the migratory fish reported by Platania et al. (1991). In the late 1980s, the water level of the lake receded leaving immense sediment deposits that decreased the gradient of the lower section of the San Juan River thereby re-

sulting in the formation of ephemeral backwaters used by early life stages of Colorado squawfish. The sediment accumulation also caused the river channel to shift from its historic bed and flow over a sandstone outcrop, creating an impassable waterfall (≥10 m at some flows) where the San Juan River now enters Lake Powell. This feature was present for approximately six years. In late spring 1995 lake levels rose high enough to inundate the waterfall once again allowing unimpeded movement of fish between Lake Powell and the San Juan River.

The presence or absence of the waterfall presents a management conundrum for Colorado squawfish in the San Juan River. As an impassable barrier, the waterfall precluded Colorado squawfish from moving upstream from Lake Powell. If there is, or was, a migratory subpopulation of Colorado squawfish that moved downstream to or through Lake Powell, it was temporarily unable to return to upstream reaches of the San Juan River. The 127 km movement recorded in 1987 (Platania et al., 1991) may have been a spawning migration by that fish from the lake to a spawning area near or below Bluff, Utah, or even to the Mixer. Thus, a potential source of spawning adults may have been eliminated, temporarily, from the San Juan River population when the waterfall was present.

However, the waterfall barrier also excluded lentic non-native predators (e.g., striped bass, *Morone saxatilis*, largemouth bass, *Micropterus salmoides*, and walleye, *Stizostedion vitreum*) from the San Juan River. Numerous striped bass, largemouth bass, and walleye were captured in the lower 83.7 km of the San Juan River during an August 1995 electrofishing trip (D. Ryden, in litt.). In addition, the low gradient in the lower 22.5 km of the river caused by sediment deposits allowed the formation of warm, ephemeral backwaters in which most of the larval and young Colorado squawfish have recently been collected (M. Buntjer et al., in litt.; K. Lashmett. in litt.). With the inundation of the waterfall, many of the nursery habitats for larval and young Colorado squawfish in the lower river have ceased to exist.

During this study basic life history knowledge has been gained on the Colorado squawfish population of the San Juan River, one of the most regulated rivers in the Upper Colorado River Basin. Many questions have been raised as well. Does our result that all Colorado squawfish were captured and remained below Cudei Diversion (km 228.5) suggest that this structure represents a behavioral barrier to upstream movement? The fact that Colorado squawfish regularly negotiate whitewater canyons such as Cataract and Westwater Canyons in the Colorado River suggest that this earth and stone diversion structure should not be a physical barrier to upstream movement. Perhaps with the small number of adult Colorado squawfish in the San Juan River, all the life history requirements of this species are being fulfilled in the 39 km reach of river (km 228.2 to 189.2) and there is no reason for these fish to move farther upstream. However, if instream diversion structures are a physical or behavioral impediment to Colorado squawfish, the efficacy of providing upstream passage via fish passage structures or the removal of instream diversions should be explored. If the Mixer represents the only suitable spawning habitat in the San Juan River, could altered flows out of Navajo Reservoir be used to help create suitable spawning areas in more upstream parts of the river, thus leading to retention of early life stages higher in the river system? Does the warmer water flowing from the Mancos River in late May and June act as a cue to initiate Colorado squawfish spawning, thereby accounting for the seasonal association of these fish with this tributary? Has the migratory component of the San Juan River Colorado squawfish population been artificially selected against by the presence of large numbers of predatory fish in Lake Powell? Was the presence of the waterfall more a benefit (eliminating lentic predators) than a detriment (impeding Colorado squawfish movements to and from Lake Powell) to San Juan River Colorado squawfish, and should flows from Navajo Reservoir and Lake Powell be managed to permanently eliminate or re-establish it? These questions should be addressed in future research efforts.

We wish to thank B. Larson, T. Sansom, K. Gido, D. Propst, and D. Jaramillo for assistance in aerial and ground tracking. Ground tracking efforts were also assisted by B. Bonar, A. Hobbes, T. Chart, B. Burdick, H. Elder, F. Pfeifer, L. Crist, M. Montagne, B. Miller, C. McAda, E. Pratts, M. Buntjer, R. Smith, and M. Trammel. Thanks to D. Propst, C. McAda and K. Bestgen for their reviews of earlier versions of this manuscript.

Literature Cited

Bestgen, K. R., and M. A. Williams. 1994. Effects of fluctuating and constant temperatures on early

development and survival of Colorado squawfish. Transactions of the American Fisheries Society 123: 574–579.

HAMMAN, R. L. 1981. Spawning and culture of Colorado squawfish in raceways. Progressive Fish-Culturist 43:173–177.

HOLDEN, P. B., AND E. J. WICK. 1982. Life history and prospects for recovery of Colorado squawfish. Pp. 98–108, *in* Fishes of the Upper Colorado River system: present and future (W. H. Miller et al., eds.). American Fisheries Society, Bethesda, Maryland.

JORDAN, D. S., AND B. W. EVERMANN. 1896. The fishes of North and Middle America: Part I. United States National Museum Bulletin No. 47. Smithsonian Institution, Washington D.C.

MCADA, C. W., AND L. R. KAEDING. 1991. Movements of adult Colorado squawfish during the spawning season in the upper Colorado River. Transactions of the American Fisheries Society 120: 339–345.

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

MINCKLEY, C. O. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix, Arizona.

MINCKLEY, C. O., AND S. W. CAROTHERS. 1979. Recent collections of the Colorado River squawfish and razorback sucker from the San Juan and Colorado rivers in New Mexico and Arizona. Southwestern Naturalist 24:686–687.

NESLER, T. P., R. T. MUTH, AND A. F. WASOWICZ. 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. American Fisheries Society Symposium 5:68–79.

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.

TYUS, H. M. 1985. Homing behavior noted for Colorado squawfish. Copeia 1985:213–215.

TYUS, H. M. 1986. Life strategies in the evolution of the Colorado squawfish (*Ptychocheilus lucius*). Great Basin Naturalist 46:656–661.

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

TYUS, H. M. 1991. Ecology and management of Colorado squawfish. Pp. 379–402, *in* Battle against extinction (W. L. Minckley and J. E. Deacon, eds.). University of Arizona Press, Tucson, Arizona.

TYUS H. M., AND C. W. MCADA. 1984. Migration, movements and habitat preferences of Colorado squawfish, *Ptychocheilus lucius*, in the Green, White, and Yampa Rivers, Colorado and Utah. Southwestern Naturalist 29:289–299.

TYUS, H. M., E. J. WICK, AND D. L. SKATES. 1981. A spawning migration of Colorado squawfish (*Ptychocheilus lucius*) in the Yampa and Green Rivers, Colorado and Utah, 1981. Proceedings of the Desert Fishes Council 13:102–108.

TYUS H. M., ET AL. 1982. Fishes of the Upper Colorado River Basin: distribution, abundance, and status. Pp. 12–70, *in* Fishes of the Upper Colorado River system: present and future (W. H. Miller et al., eds.). American Fisheries Society, Bethesda, Maryland.

WICK, E. J., D. L. STONEBURNER, AND J. A. HAWKINS. 1983. Observations on the ecology of Colorado squawfish (*Ptychocheilus lucius*) in the Yampa River, Colorado, 1982. United States National Park Service, Water Resources Field Support Laboratory, Technical Report 83-7, Fort Collins, Colorado.

WYDOSKI, R. S., AND J. HAMILL. 1991. Evolution of a Cooperative Recovery Program for the Endangered Fishes in the Upper Colorado River Basin. Pp. 123–135, *in* Battle against extinction (W. L. Minckley and J. E. Deacon, eds.). University of Arizona Press, Tucson, Arizona.

UNITED STATES DEPARTMENT OF THE INTERIOR. 1974. Endangered and threatened wildlife and plants; animal notice of review. Federal Register 39(3):III–75A.

U.S. FISH AND WILDLIFE SERVICE. 1990. Colorado squawfish recovery plan. United States Fish and Wildlife Service, Denver, Colorado.