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LIFE HISTORY AND PROSPECTS FOR RECOVERY OF COLORADO SQUAWFISH

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ABSTRACT

The endangered Colorado squawfish, *Ptychocheilus lucius*, is restricted to the Green, Yampa, and White rivers in Colorado and Utah and the mainstem Colorado River below Grand Junction, Colorado. Habitat preferences of these long-lived large-river fish change with age, season, and habitat availability. Relatively little is known about their growth and movements. Prespawning temperatures and flows are major determiners of reproductive success. Dam construction was the main reason for squawfish declines in the Upper Colorado River Basin. Reproducing populations remain relatively large only in the Green River System. Prospects for recovery in areas with potentially good habitat are bright from a biological viewpoint, but meager possibilities of assuring adequate streamflows in the future seem a major obstacle to recovery in natural ecosystems of the Upper Basin. *(Editors' abstract)*

INTRODUCTION

The Colorado squawfish *(Ptychocheilus lucius)* is North America's largest native cyprinid, at one time reaching 1.5-2.0 m and 35-45 kg. It was used as food by Indians and early white settlers. Early distributional records established its range throughout the Colorado River System in the main channels and larger tributaries (Girard 1856; Jordan 1891; Jordan and Evermann 1896; Gilbert and Scofield 1898; Ellis 1914). Very few published accounts of the species exist for the first half of the 20th Century. In the 1960's the construction of large dams that threatened the river and its inhabitants spurred investigation of this species and the other rare fish. The Colorado squawfish is the most studied of the four rare, large-river endemics, probably due to its more widespread occurrence and its economic link with the past history of the West.

The Colorado squawfish is one of four species of *Ptychocheilus*, all found in western North America. The Sacramento squawfish *(P. grandis)* is endemic to the Sacramento River System in California. The Umpqua squawfish *(P. umpquae)* is found only in the Umpqua and Siuislaw rivers of Oregon, and the northern squawfish *(P. oregonensis)* is found in the Columbia River and other coastal streams in Washington and Oregon. Of the four, only the northern squawfish is abundant, scorned as a predator on gamefish and the target of specific poisons and other eradication techniques.

The Colorado squawfish was very common at one time, abundant enough to be pitchforked out of irrigation canals in Arizona (Miller 1961). Presently it is extinct in the Colorado System below Glen Caynon Dam (Minckley 1973), the Green River above Flaming Gorge Dam (Baxter and Simon 1970), and the San Juan River in New Mexico (Frontis.). The Green River System of Colorado and Utah, including the Yampa and White rivers, and the main-stem Colorado River below Grand Junction, Colorado harbor the last remaining populations. One juvenile was recently captured in the San Juan River of Utah (VTN 1978). Reproductive success is highest in the Green River (Holden and Stalnaker 1975a).

This paper will discuss what is presently known concerning Colorado squawfish life history and the chances for survival of this unique animal. Many of the recent findings on this species have not been formally published but are contained in readily-available reports from various agencies and private concerns. An extremely intensive study on this species is presently being conducted by the U.S. Fish and Wildlife Service (FWS). One of us (Wick) has been involved in this study, and some general observations are included in this report. More detailed data should be available in 1982 when FWS completes its study (Miller *et al.* 1982a, b).

LIFE HISTORY AND BIOLOGY

Age and Growth

Vanicek and Kramer (1969) provided the first comprehensive information on age and growth of Colorado squawfish. Their mean calculated total lengths for 658 fish from the upper Green River showed that young squawfish grew about 50 mm per year until after year 3, when annual increments increased for a couple of years and then decreased as the fish became larger. Three-year-old fish were about 162 mm total length, age 4 fish were 238 mm, age 5 fish, 320 mm, and age 8 fish, 499 mm. Seethaler (1978) found similar growth rates for older fish from the Colorado and Yampa rivers.

Fish from the lower Green River, where water temperatures warm earlier each year, probably grow faster. Holden (1977) found young-of-the-year in Gray Canyon were larger than those reported by Vanicek and Kramer (1969) from the upper Green River at about the same age.

Colorado squawfish are long-lived fish; Vanicek and Kramer (1969) found an 11-year-old, 610-mm female. Since fish of 700-900 mm have recently been caught, and the old reports of 2-m specimens appear valid, the potential life of Colorado squawfish must be 20-50 years or more.

Length-Weight Relationship

The Colorado squawfish is a relatively elongated, very pike-like fish. Fish under 400 mm are often quite thin. Vanicek and Kramer (1969) reported a weight-length relationship of $\log W = -5.4177 + 3.126 \log L$ for fish from the upper Green River. Seethaler (1978) calculated similar relationships for Colorado squawfish from the Colorado and Yampa-Green rivers. This indicates that the weight of Colorado squawfish increases slightly faster than the cube of the length (Vanicek and Kramer 1969).

Food Habits

Young Colorado squawfish start eating small crustaceans (copepods and cladocerans) and small aquatic insect larvae (chironomids), gradually increasing the size of food items (insects) until they are about 100 mm in length; then fish become the major food item. They become almost entirely piscivorous after 200 mm (Vanicek and Kramer 1969). Little is known about major prey species of fish. Vanicek and Kramer (1969) found remains of redside shiners *(Richardsonius balteatus)*, an introduced species, most prevalent. It would appear that young of flannelmouth sucker *(Catostomus latipinnis)* and bluehead sucker *(Pantosteus discobolus)*[1], the two most abundant native species throughout most of the Upper Colorado River Basin, were probably the most common natural prey species. The present abundance of introduced cyprinids [red shiner *(Notropis lutrensis)* and redside shiner] has probably provided additional prey. Recurrent stories of large, dead Colorado squawfish with channel catfish *(Ictalurus punctatus)* wedged in their throats suggest this predator probably feeds on whatever it can catch, including at least this one deadly exotic.

Habitat Requirements

The Colorado squawfish has always been considered a "large river" fish and is seldom found in small tributaries. They inhabit the larger and medium-sized tributaries, including the Yampa, White, Duchesne, Dolores, and Gunnison rivers (Frontis.). No actual size definition has ever been attempted, to our knowledge, to determine if river size is actually a requirement. Adults have been found in the mouths, or short distances upstream, of several small streams along the Green River during high-runoff periods. Habitat formed when the mouths of these streams are dammed by the Green River appears to be preferred.

In many of the tributaries that Colorado squawfish utilize, their upstream range is usually at the lower end of the trout (cold-water) zone. In the Green River of Wyoming, Colorado squawfish were reported to Green River, Wyoming, but not above. In the Yampa River, only one has been taken above Craig, Colorado. In the Gunnison River, Delta, Colorado appears to have been the upstream range of this species, although recently they have not been found this far upstream. Therefore, stream size and summer temperatures appear to be determining factors in habitat selection.

Stream areas used by Colorado squawfish have been intensively studied in recent years. Young squawfish (1-, 2-, and 3-year-old fish) prefer backwaters and other areas with slow current and (usually) a silt or silt-sand substrate (Fig. 1) (Vanicek and Kramer 1969; Holden and Stalnaker 1975a; Holden 1977; Twedt and Holden 1980). Changes in habitat selection during various seasons have not been noted. It is highly probable that flowing portions of the river are utilized during winter, since many backwaters are frozen solid.

Larvae in the Yampa and Upper Colorado rivers are found in a variety of calm habitats, often alongside rather swift currents. Since neither of these rivers has many good backwaters, the larvae probably find the best available habitat and drift downstream looking for better habitat.

As Colorado squawfish become larger (150-200 mm), numbers caught drop dramatically (Holden 1977; Holden and Selby 1979). This same phenomenon was noted by McAda (1977) for juvenile suckers. It appears that this is the size at which these fish begin using the main river channels; hence, they become much more difficult to sample. Food habits changes, from insects and crustaceans (most common in backwater areas) to fish that are found in a larger variety of habitats, also suggest a move. The ability of juveniles to maneuver in the main channels is probably also enhanced after they reach about 200 mm in length.

Adult habitat preferences change with season as well as with the habitat available. Twedt and Holden (1980) summarized much of the available data and categorized habitat preferences for substrate, depth, velocity, and cover for pre-runoff, runoff, and post-runoff periods (Figs. 2, 3, 4). These data indicate that adults prefer run habitat along shores of medium depth during pre- and post-runoff periods. They prefer backwaters during high-flow periods, although runs are also used during this time. This same general pattern was noted in the Yampa River in 1981 (Miller *et al.* 1982a). Adult squawfish were found in eddies and near mouths of irrigation returns (as well as along the shorelines of runs) during pre-runoff, sought out large back-

[1]The authors do not agree with the change of the generic name to *Catostomus*, as proposed in the *List of Common and Scientific Names of Fishes* published by the American Fisheries Society.

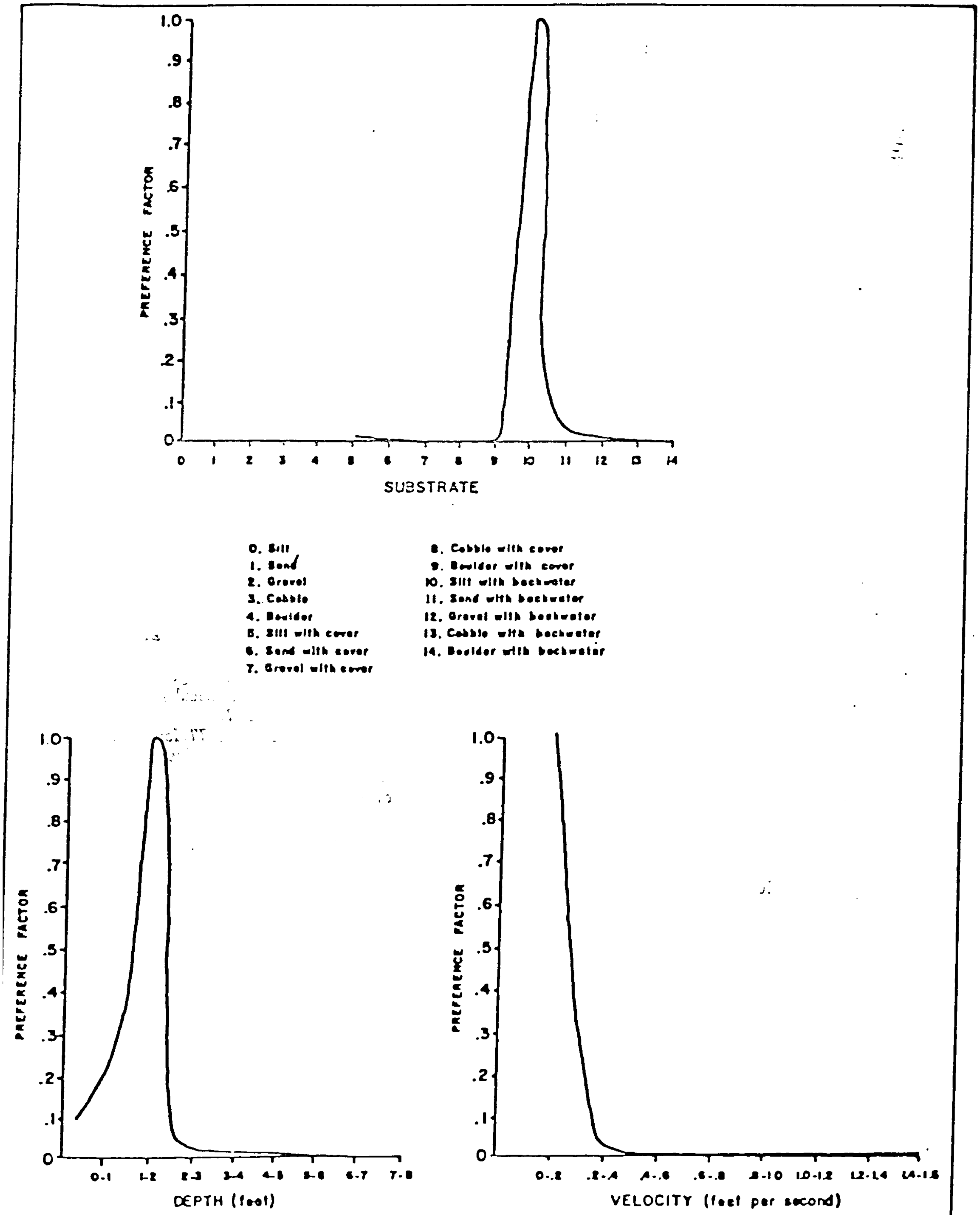


Figure 1. Habitat suitability curves for young-of-the-year and juvenile Colorado squawfish (from Twedt and Holden 1980).

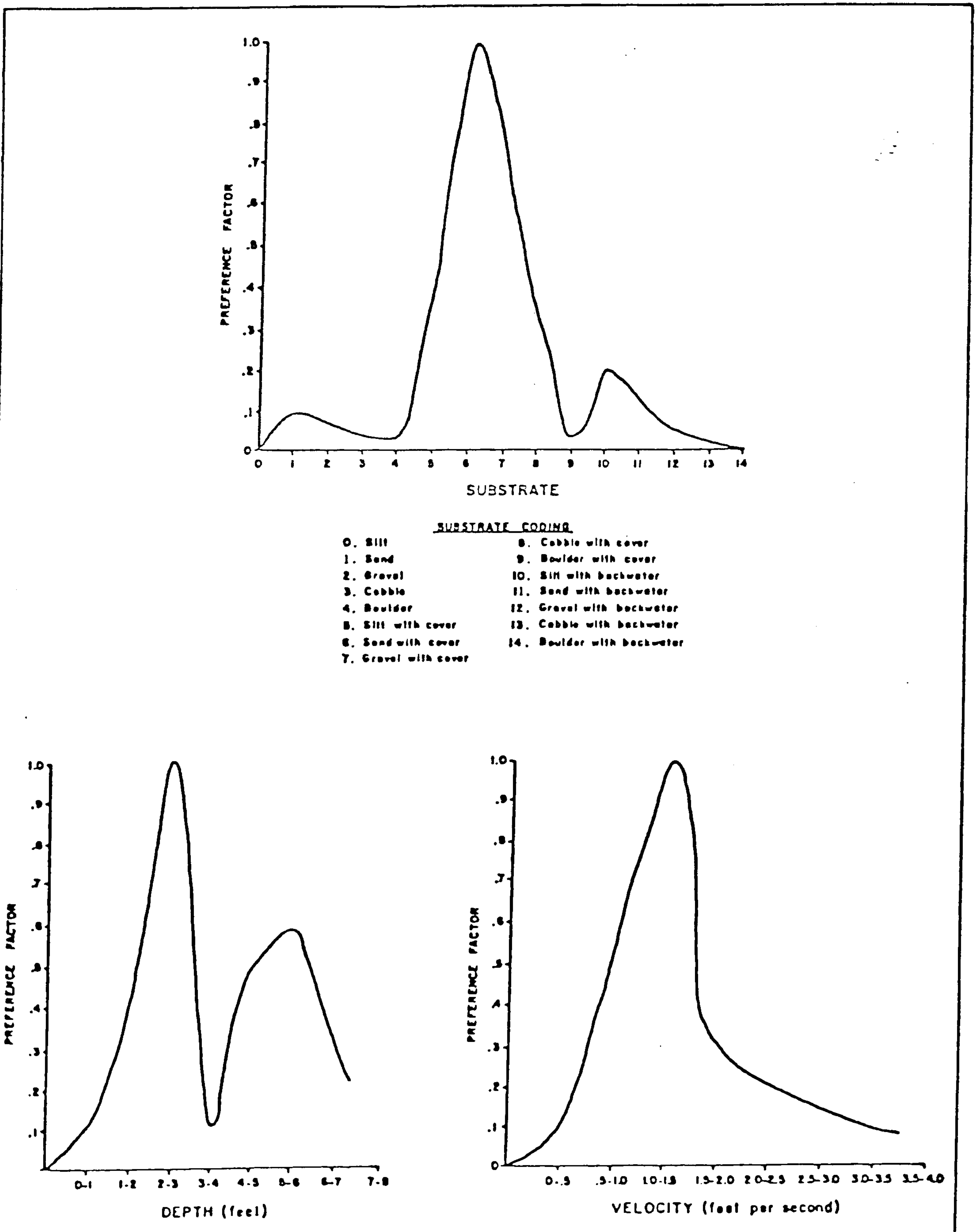
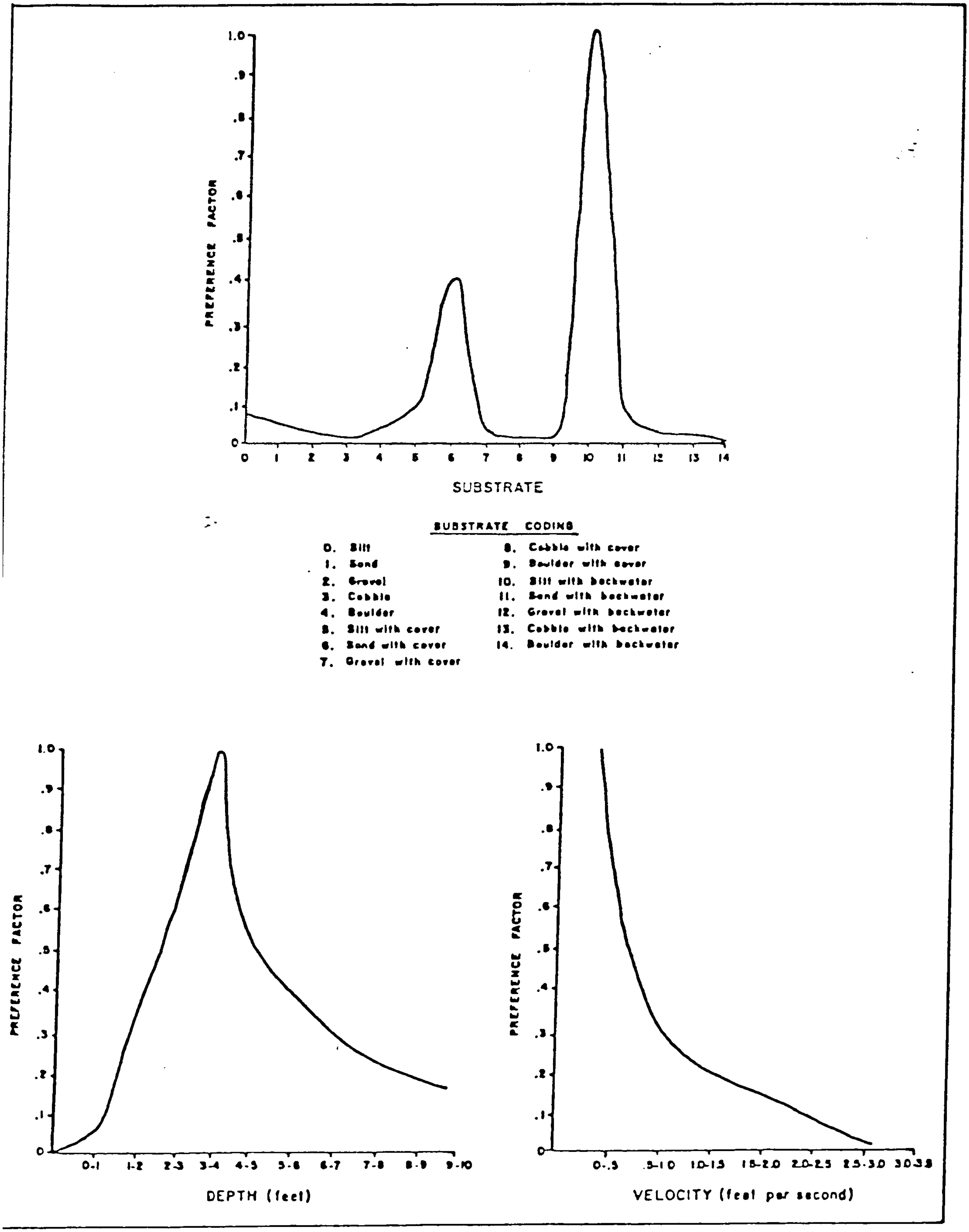


Figure 2. Habitat suitability curves for adult Colorado squawfish during the pre-runoff season (from Twedt and Holden 1980).



gure 3. Habitat suitability curves for adult Colorado squawfish during the runoff season (from Twedt and Holden 1980).

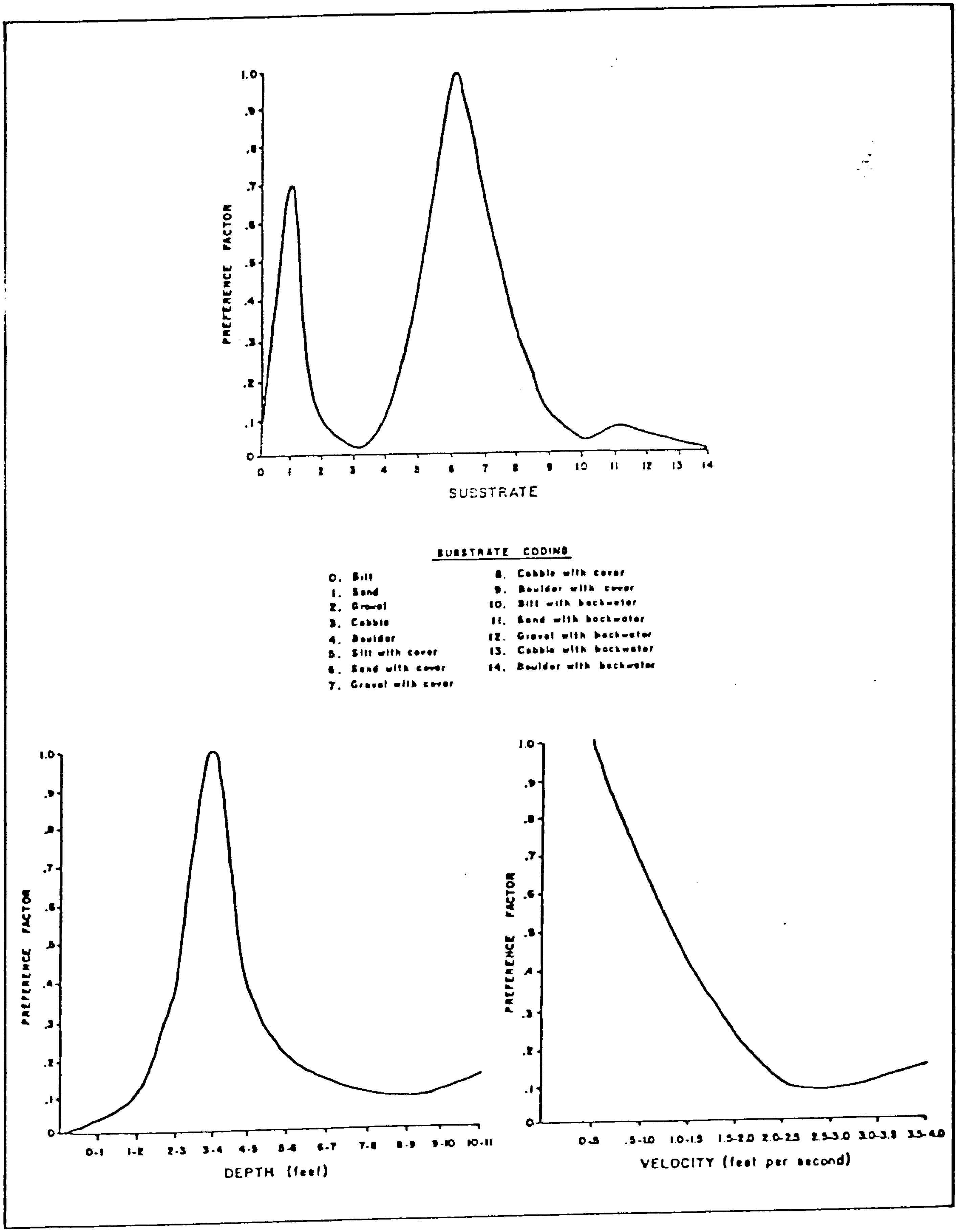


Figure 4. Habitat suitability curves for adult Colorado squawfish during the post-runoff season (from Twedt and Holden 1980).

waters during runoff, and utilized deep holes and diverse habitats in post-runoff periods. Habitat preference curves have been constructed by the Cooperative Instream Flow Service Group (Miller *et al.* 1982b), and are in general agreement with those shown here.

Valdez *et al.* (1982) presented habitat curves for 34 adult squawfish collected in the Colorado River in 1979. Those curves indicate a preference for boulder-bedrock substrate and some smaller preference for deep areas (20-30 ft; 6-9 m). The fish used in that analysis primarily came from Black Rocks, a deep, incised, 0.25-mile (0.40 km) portion of the Colorado River with an extruded black schist substrate. Since that area is unusual, and similar habitat is not generally available in other portions of the Upper Colorado Basin, these data must be used with caution when projecting habitat availability in other areas. This raises the general question: Is there a dramatic variation in habitat preference between portions of the Upper Basin? The answer appears to be no, although some local preference changes do occur with the type of habitat available.

Movement

Many accounts of Colorado squawfish "spawning migrations" can be found in the early literature and in discussions with "old timers" (Minckley 1973), and movement of large numbers of ripe males into the Yampa River during mid- and late summer was observed in squawfish from the upper Yampa River in 1968-1970 (Holden and Stalnaker 1975b). In 1981, radio-tagged adult Colorado squawfish from the upper Yampa River moved as much as 145 km downstream to the lower Yampa (Tyus *et al.* 1982). Other adults tagged in the Green River moved upstream about 80 km into the Yampa River. These radio-tagged fish were located near several ripe males and a female that had apparently just spawned. The seasonal increase in adult numbers in the Yampa River was also noted by Seethaler (1978). The probable reason for this movement into the Yampa is for spawning, as noted by Tyus *et al.* (1982). Holden (1977) suggested that spawning occurred at various locations in the Green River as evidenced by location of young-of-the-year. This indicates that migrations may not be very long, that all fish may not move to spawn, and that spawning occurs at several locations in the Green River System.

Daily (short-term) movements are poorly understood. A general pattern of movement at dawn or dusk has been noted by a number of researchers; catch rate increases at these times. Radiotelemetry studies by FWS (Miller *et al.* 1982b) have indicated most adult Colorado squawfish select rather sheltered areas near shore, to which they often return after moving about a section of river. These short-term movements are intensified during dawn and dusk. This suggests that adults may move about to feed, which might be expected for a piscivore in a turbid river.

Mark-recapture efforts have not provided much data on movement, although many adult Colorado squawfish have been tagged. Holden and Crist (1981) recaptured one adult Colorado squawfish near Jensen, Utah that had moved less than 1 km in more than a month. Another adult was tagged near Jensen by FWS in August 1979 and was recaptured in the Yampa River in October 1980 (Wick *et al.* 1981). The FWS (Tyus *et al.* 1982) recaptured two Colorado squawfish in the Yampa River in 1981 that had been tagged in the Yampa River 65-130 km upstream. Another fish had originally been tagged near Ouray, in the Green River, and was recaptured in the upper Yampa River, 173 km above its mouth. The two Green River fish moved considerable distances upstream. Recent radiotelemetry studies by FWS (Tyus *et al.* 1981) have shown that some adults move very little for rather long periods of time (1-2 months), others move more regularly, and sudden movements of over several hundred km up- or downstream occur.

Movements of young fish in a backwater studied by Holden (1977) suggested considerable movement either within a backwater or between the main channel and the backwater. This was based on a mark-recapture study for 2.5 days. The FWS is presently studying young fish movement, and they have found a daily movement pattern in and out of backwaters (Charles McAda, U.S. Fish and Wildlife Service, Vernal, Utah, 1980 pers. comm.). Just where the young fish are when they are not in the backwater has not been determined.

To our knowledge, there are no data to suggest how far downstream young Colorado squawfish move after hatching. Holden and Crist (1981) suggested downstream drift was not for long distances but probably lasted only until suitable habitat was reached. Bill Pearson (University of Louisville, Louisville, Kentucky, 1980 pers. comm.) studied invertebrate drift in the Green River in the mid-1960's; he caught no larval fish and saw only one fish egg in his nets. Recent collections of larval and young-of-the-year Colorado squawfish in the Yampa and Upper Colorado rivers (Miller *et al.* 1982b) suggest some downstream movement, perhaps as much as 150 km, may be occurring. Collections of young-of-the-year for the past 15 years (Vanicek and Kramer 1969; Holden and Stalnaker 1975a; Holden 1977) in the Colorado and Green rivers do not support a hypothesis of long-distance downstream movement by larvae. These data, along with general observation in the field, suggest downstream larval fish movement of all the native species of fish in the Upper Colorado System did not evolve as a reproductive or distributional attribute but may be used by young to locate acceptable habitat. Movement may be greatest in areas of marginal habitat, such as the Colorado River in Colorado, where streamflow has been greatly reduced and backwater habitat is relatively scarce.

Reproduction and Early Life History

Colorado squawfish mature in 5-7 years (Vanicek and Kramer 1969; Seethaler 1978). Hamman (1980) stated that captively-spawned and reared Colorado squawfish males and females matured in 5 and 6 years, respectively. Spawning occurs when river temperatures are about 20 C (Holden and Stalnaker 1975b), usually in July and August, in the Upper Colorado Basin. Spawning behavior has never been observed in the wild, but Hamman (1980) observed spawning of captive fish at Willow Beach National Fish Hatchery. Two males nudged a female's vent, causing her to vibrate and release eggs while the males extruded milt. The adhesive eggs were broadcast with little regard for substrate, and the spawning act was repeated several times. Spawning took place over a 48-hour period in shallow depths (20-55 cm), and the eggs hatched in 96 hours in 20 C water. The young fish fed on natural crustacean plankton in the raceways and were 48-55 mm in length in 110 days.

Observation of Colorado squawfish in the Yampa River in 1981 (Miller *et al.* 1982b) suggested spawning occurs over riffles, adults spawn in fairly large groups of males (8-10) with fewer females, and they reside in adjacent pools between spawning runs. The preponderance of males over females, especially during spawning time, has been noted by several authors (Holden and Stalnaker 1975b; Seethaler 1978). This is also the case with northern squawfish (McPhail and Lindsey 1970).

Prespawning temperatures and flows appear to be important in determining reproductive success in Colorado squawfish. Vanicek and Kramer (1969) indicated that Colorado squawfish did not spawn in the Green River in the cool tailwaters of Flaming Gorge Dam from 1964 to 1966 because temperatures were not adequate. They did find young, evidence of successful reproduction, in the Green River of Dinosaur National Monument below the mouth of the Yampa River and hypothesized the natural temperatures of the Yampa ameliorated the cool flows of the Green River. Holden and Stalnaker (1975a) and Seethaler *et al.* (1979) sampled the Green River in Dinosaur National Monument and found no young Colorado squawfish below the mouth of the Yampa in 1968-1971 and 1974-1976, respectively. Holden (1980) and Holden and Crist (1981) showed that this lack of reproductive success was correlated with higher, and therefore colder, flows from Flaming Gorge Dam after 1966. These flows were apparently too large to be ameliorated by the Yampa River.

Young Colorado squawfish were again found in Dinosaur National Monument below the Yampa's mouth in 1980, following inlet modification of Flaming Gorge Dam that raised tailwater temperatures. Young Colorado squawfish were also found in the lower 15.3 km of the Yampa River in 1980 and may have been the source of the young Colorado squawfish found immediately below the confluence. Holden and Crist (1981) hypothesized that adult Colorado squawfish that lived in the Green River moved into the Yampa to spawn. But spring and summer river temperatures after 1966 were too low to allow proper egg maturation in the females. The inlet modification of Flaming Gorge Dam warmed the river sufficiently for successful spawning in the lower Yampa River and the Green River of Dinosaur National Monument.

This hypothesis indicates that rather small changes in temperature during an apparently critical stage, egg maturation in the female, may determine reproductive success. Observations in 1981 (Tyus *et al.* 1982) showed that many of the fish spawning in the Yampa River originated from the upper Yampa, not the Green River. Therefore, the above hypothesis does not fully resolve this dilemma, and more information will be required to determine all the factors necessary for good reproductive success.

Holden (1977) did not find young-of-the-year Colorado squawfish in the Green River from Jensen to Gray Canyon in 1977, a drought year. Holden and Crist (1981) did not find any 1977-year-class fish near Jensen in either 1978 or 1979, and Holden and Selby (1979) found only one potential 1977 fish during extensive sampling in 1979. Holden (1980) showed the river temperature in 1977 at the Jensen U.S. Geological Survey gage did not indicate an abnormally cool year; in fact, good Colorado squawfish reproductive success occurred in several colder years. Flow, primarily the lack of a high spring peak in 1977, was apparently the reason for unsuccessful Colorado squawfish reproduction. Colorado squawfish reproduction was noted in 1981 (Miller *et al.* 1982b) in the Yampa River, another low-flow year, although the relative success as indicated by abundance of young-of-the-year has not been determined.

Other data suggest that high spring flow is important to successful Colorado squawfish reproduction. Dams of the Wayne N. Aspinall Unit were completed on the Gunnison River in 1964 and reduced spring flows after that time (Joseph *et al.* 1977). Taba *et al.* (1965) found young-of-the-year Colorado squawfish to be quite abundant near Moab, on the Colorado River, in 1962-1964. Holden and Stalnaker (1975a) found only three juveniles near Moab in 1971 and none in 1968-1970. Kidd (1977) did not find young Colorado squawfish in the Colorado River near Grand Junction. These data indicate a major reduction in young Colorado squawfish numbers coincidentally with reduced flows caused by Wayne N. Aspinall Unit dams. Valdez and Mangan (1981) found young Colorado squawfish near Moab, but not in the numbers reported by Taba *et al.* (1965). Young-of-the-year Colorado squawfish were also caught just below Grand Junction in 1979 and 1980, but numbers were also low (Wick *et al.* 1981). This all suggests that Colorado squawfish reproductive success in the Colorado River probably was affected by altered flows, with the loss of spring flows having a major effect.

Therefore, temperature and flow, and probably the combination of these two factors, appear to be extremely important to the reproductive success of Colorado squawfish. Additional study is needed to clarify this relationship because poor, or total loss of, reproductive success is the major problem facing this species in the Colorado River Basin.

Disease and Parasites

Colorado squawfish are infested with a number of parasites. The external copepod *Lernea* is common on juveniles and adults. Vanicek (1967) found a tapeworm *(Proteocephalus)* in 65% of the Colorado squawfish over 200 mm he examined. Seethaler (1978) indicated that the protozoan *Myxobolus* has been found on the gills of Colorado squawfish from the Green River. Seethaler (1978) also stated that *Lernea* was most abundant on Colorado squawfish from Walter Walker Wildlife Refuge, an abandoned gravel pit along the Colorado River near Grand Junction, Colorado. Seethaler (1978) suggested that parasites such as *Lernea* were introduced to the Colorado River system with exotic fishes, and Flagg (1980) supported this hypothesis by noting that the introduced fishes were more parasitized than native forms.

Population Decline

The construction of Colorado River Storage Project dams (Flaming Gorge, Glen Canyon, Wayne N. Aspinall Unit, Navajo Dam) in the 1960's was the major reason for the decline of Colorado squawfish in the Upper Colorado Basin. A number of authors have pointed this out, including Miller (1963), Holden and Stalnaker (1975a), and Seethaler (1978). Holden (1979) summarized the effects of these dams as they are currently understood.

1. Preimpoundment eradication programs were responsible for extinction of Colorado squawfish in the Green River above Flaming Gorge Dam, and they probably caused reductions in numbers in Dinosaur National Monument and loss of populations in the San Juan River.
2. Habitat loss due to reservoir construction was responsible for loss of the Colorado River under Lake Powell (Glen Canyon Dam) as viable Colorado squawfish habitat.
3. Loss of habitat below dams due to cold flows was responsible for loss of 105 km of habitat below Flaming Gorge.
4. Loss of reproductive success due to altered temperatures and/or flows was responsible for declines in reproductive success in the Green and Yampa rivers in Dinosaur National Monument from 1966 to 1980 and in the Colorado and Gunnison rivers of Colorado and Utah.
5. Loss of habitat, especially backwaters for young, due to reduced spring flows and fluctuations for power generation during low-flow periods, was also a factor.

Several other factors have been suggested as affecting Colorado squawfish populations, including predation-competition from exotics, disease and parasites, and changes in water quality (Seethaler 1978). We suspect these are complicating factors that only affect Colorado squawfish in marginal habitat conditions caused by dams and other water-depletion developments.

CHANCES FOR SURVIVAL

Colorado squawfish populations in the Green River System (including the Yampa and White rivers) are relatively large, as evidenced by few recaptures of tagged adults (Miller *et al.* 1982a). Reproduction has been consistent for most of the last 10-15 years in the Green River. If the Colorado River population could reproduce as successfully as the Green River stock, recovery would be nearly complete in the remaining potentially good habitat. Establishment of other populations may be possible, especially in the San Juan River, after we know more about reproductive and habitat requirements. Artificial propagation can readily supply young or adult fish for transplanting. Therefore, biologically, the outlook appears to be optimistic.

Unfortunately, demands on the water of the Upper Colorado River Basin are great, and chances of protecting sufficient flows for the future appear low. Protection of Upper Colorado Basin flows is no longer being attempted by the cognizant federal agencies, and basic Colorado squawfish requirements are being lost just as we are learning the factors important to their continued survival. Hopefully we can learn enough to prevent this unique species from becoming a hatchery-reared entity, an untenable situation for those who appreciate natural ecosystems.

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