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Life strategies in the evolution of the Colorado squawfish (*Ptychocheilus lucius*)

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LIFE STRATEGIES IN THE EVOLUTION OF THE COLORADO SQUAWFISH (*PTYCHOCHEILUS LUCIUS*)

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ABSTRACT.—The Colorado squawfish, a large predaceous cyprinid, is a generalist species adapted to the large seasonal water fluctuations, low food base, and changing riverine subsystems of the Colorado River. Extant at least as early as the Miocene epoch, *Ptychocheilus* has survived by incorporating life strategies to deal with changing climates varying from arid to pluvial. Migration and long-term movement patterns appear to have evolved as tactics to perpetuate a grand reproductive strategy for exploiting the changing habitats and general environmental conditions of the late Cenozoic era. Accordingly, high mobility of a large fish would aid in selection of optimum spawning, nursery, and adult habitats in the dynamic lacustrine/riverine system that existed at that time. A spatial separation of life stages thus produced would aid in the reduction of intraspecific competition. Large size, long life, and late spawning of *Ptychocheilus* indicate that mortality of young must be disproportionately high compared to that of the adult form. Growth to a large size should reduce predation by other fishes and, once attained, would facilitate long distance movement for reproduction, feeding, and other purposes. Such a strategy, formerly highly adaptive, may now be implicated in the decline of this species in controlled riverine systems.

The genus *Ptychocheilus* includes the largest cyprinids in North America. Represented by four species today, the largest of these, the Colorado squawfish (*Ptychocheilus lucius* Girard) formerly grew to a size of about 1.8 m and 45 kg (Miller 1961). Endemic to the Colorado River Basin, this fish, once distributed throughout the basin, has declined since the 1930s and is today restricted to the upper Colorado River Basin, where it is classified as endangered by the U.S. Fish and Wildlife Service (1973, 1974). The loss of the Colorado squawfish from parts of the Colorado River is apparently related to major water developments that have ostensibly reduced *P. lucius* to about 25% of its former range (Tyus 1984). Although many workers have postulated man-induced changes in riverine conditions as primary factors in the reduction of the range and abundance of this species (Miller 1961, Holden and Wick 1982, Ono et al. 1983), a lack of basic knowledge about its life history, especially in locations where the fish has been lost (Minckley, 1973), has made these implications impossible to prove. Recent research in the Green River Basin (Fig. 1) by the U.S. Fish and Wildlife Service (Tyus and McAda 1984) resulted in the first discovery of a spawning grounds of this species in 1981 and identified migrations and movements as important factors in the reproductive strategy of this species. These findings have been substantiated by the work of Haynes et al. (1984), Wick et al. (1983), Tyus (1985), and others.

With the present knowledge of the life history requirements of *P. lucius*, it is now possible to relate its apparent life strategies with its evolution and adaptations to conditions in the Colorado River Basin. In so doing I have drawn heavily from the works of G. R. Smith (1981) and M. L. Smith (1981), who presented the background on late Cenozoic climates and adaptations of the southwestern fish fauna, particularly *P. lucius*, upon which this work is based.

CLIMATE AND ADAPTATION OF *PTYCHOCHEILUS*

The cyprinid fishes apparently arrived in the New World from Asia in the Miocene epoch, and fossil *Ptychocheilus* species similar to modern *Ptychocheilus lucius* have been reported from the middle Pliocene in the Colorado River system of northern Arizona (Miller 1961). *Ptychocheilus* had widespread distribution in the Pliocene, as evidenced by fossils in Lake Idaho (Smith 1975), the Great Basin (G. Smith 1981), and Arizona (Miller 1961). Furthermore, the similarity between the Pliocene fossils and modern forms suggests that the adaptation to swift water habitat had

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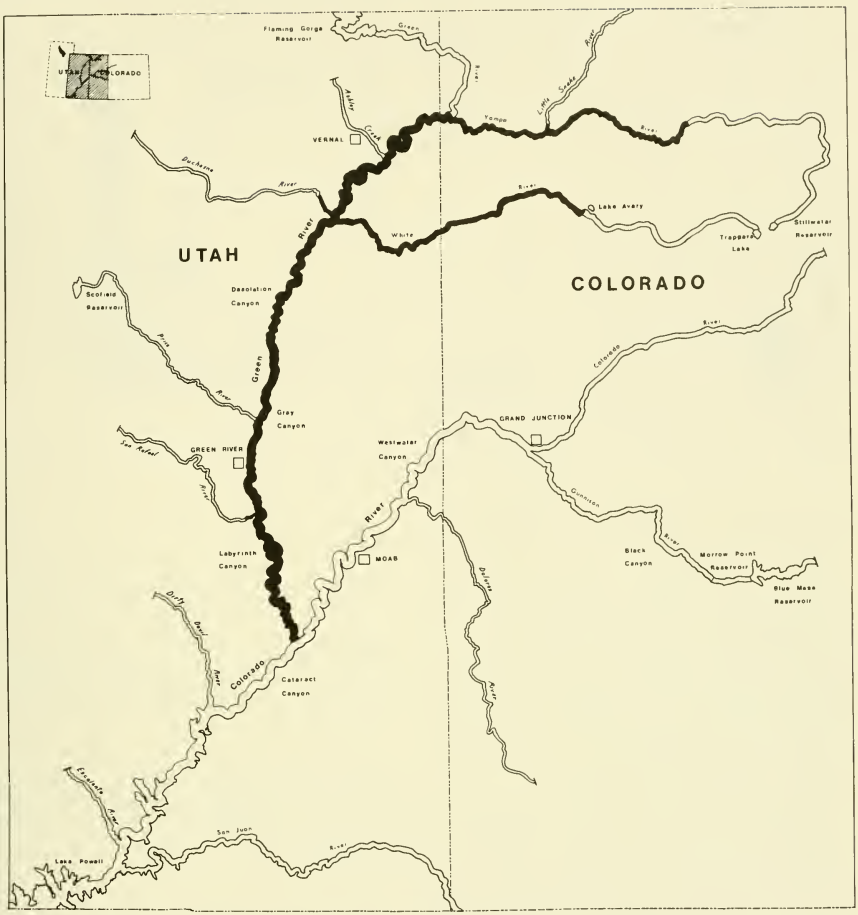

Fig. 1. Upper Colorado River Basin and Green River study area (shaded).

occurred in *Ptychocheilus* by the mid-Pliocene (Miller 1961). Nonetheless, the largest *Ptychocheilus* reported in the fossil record lived in Pliocene Lake Idaho (Smith 1975), indicating that *Ptychocheilus* successfully utilized both riverine and lacustrine systems.

The Southwestern United States is more arid today than in the Late Cenozoic, and this increasing aridity no doubt resulted in the loss or reduction of lacustrine habitats and the extinction of lake dwelling salmonids and centrarchids from the Colorado River system. This change was progressive from the Pliocene, when a system of lakes covered the lower and upper Colorado River Basins, and persisted during pluvial periods until the Pleistocene. During this epoch the life history of fishes was remarkably impacted by such long pluvial periods interrupted by short periods of desert conditions (G. Smith 1981).

An evaluation of the fish fauna of the Colorado River in recent times (before introductions by man) might lead one to conclude that

the isolated drainages and depauperate faunas of today reflect Cenozoic conditions. They do not. Instead, the fossil record shows that the large regional desert environs of the Southwest are "geologically new" (M. Smith 1981) and not typical in the development of life history attributes of the fish fauna. This has led M. Smith (1981) to propose that the ecological history of the fishes suggests they should be considered generalists, not specialist species. In this case *Ptychocheilus* would have developed the capability to utilize both riverine and lacustrine habitat depending upon the climatic conditions prevailing.

During the late Cenozoic, estuarine conditions in the lower basin and widespread lacustrine habitat during pluvial periods would provide eutrophic conditions that could be exploited by a top carnivore like *Ptychocheilus*. These same areas, however, might not have provided the best spawning and nursery conditions because of adverse environmental (e.g., oxygen, substrate) and biological (e.g., predation) factors. If *Ptychocheilus* could move between preferred spawning and feeding areas, it might have the best of both. G. Smith (1981) proposed that migration would be a major adaptation to dry seasons for intermountain desert fishes like *Ptychocheilus*, and that emigration of young fish to unoccupied areas might be selected for in genotypes. If movement and/or migration is highly adaptive, this behavior would have evolved with modern *Ptychocheilus*.

Another consideration in the evolution of *Ptychocheilus* is large adult size. The popular notion of a richer food supply in the recent past is interesting, but is probably not the factor driving the adaptation to large body size. In the intermountain desert G. Smith (1981) noted the tendency for large habitats to produce large fishes, and, in view of the low food ration available, suggested that life history adaptations to the growing season and differential mortality are primary determinants. Species experiencing low adult mortality that grow larger and live longer could be expected to produce a large number of offspring in the desirable wet years and outcompete those species that sacrifice size and longevity for early reproduction. Since *Ptychocheilus* and various salmonids are the only large native predators throughout most of the Colorado River, survival to a moderate size would insure low adult mortality. Thus, modern *Ptychocheilus* should display rapid growth and delayed reproduction to favor a large adult size if these attributes have selective advantage.

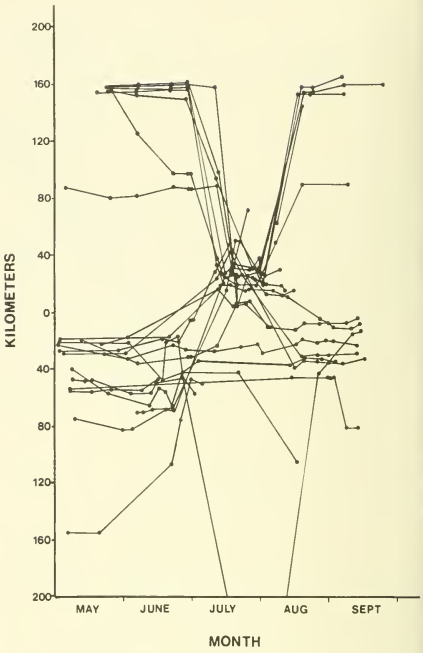

Fig. 2. Movement of radiotelemetered Colorado squawfish, Yampa and Green rivers, 1983 and 1984 (after Archer et al. 1985). Mouth of Yampa River = 0 km.

STRATEGIES OF *PTYCHOCHEILUS LUCIUS*

As stated previously, modern *Ptychocheilus* exists today in conditions different from those in which it evolved. An examination of the known life history attributes of *P. lucius* contrasted with the conditions and potential adaptations to late Cenozoic conditions may reveal life strategies in its evolution that would aid in its survival and potential recovery.

Migration, Movement, and Habitat Selection

As predicted by G. Smith (1981), *P. lucius* makes extensive use of migration in its life

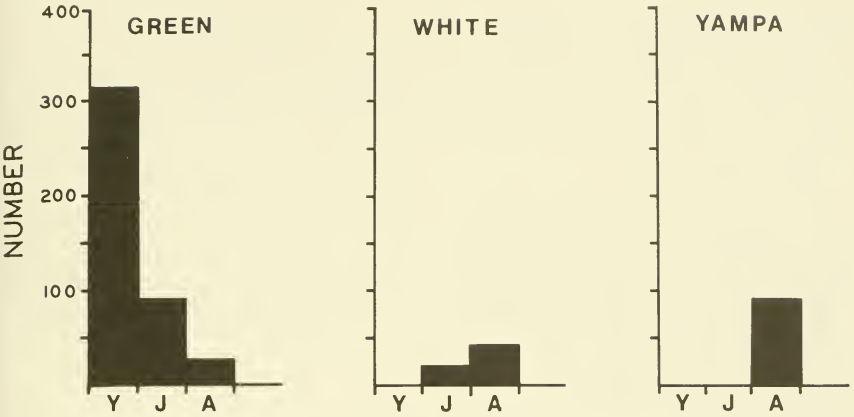

Fig. 3. Catch of Colorado squawfish from the Green, White, and Yampa rivers (Tyus et al. 1982, Miller et al., *White River*, 1982; *Yampa River*, 1982. Y = young of year, J = juveniles, A = adult.

strategy, and adults have been documented as homing to desirable spawning sites (Tyus 1985). Figure 2 illustrates the spectacular spawning migrations to the Yampa River spawning site in 1983 and 1984. Migrations of young are not so easily documented, but downstream transport of larvae have been noted by Haynes et al. (1984) and Tyus and McAda (1984). A net long-term movement of juveniles must occur to populate adult areas upstream, probably in the late young-adult stage, is indicated by collection data (Tyus et al. 1982). Figure 3 illustrates that, in the mainstem Green River, young *P. lucius* are relatively abundant and juveniles common; however, in the major tributaries (White and Yampa rivers) where adults predominate, juveniles are rare and young absent during most of the year.

Habitat selection appears to be the driving force for migration. Hence, adults move up to 200 km to spawn in white-water canyons. After hatching, young larvae can drift downstream and occupy warm shallow habitats where rapid growth is possible. These movements also aid in reducing intraspecific predation since the adults and young tend to concentrate in different river sections. Recent studies (Archer et al. 1985) also show that during flood periods adult *P. lucius* move out of the river banks and occupy flooded bottoms, where they presumably feed on terrestrial wildlife such as small mammals (Beckman 1952).

Potamodromous migrations of cyprinid fishes are not well documented for North American forms, at least not for migrations of 100 km or more. Such migrations are not uncommon in flood plain rivers in other parts of the world (Welcomme 1979). *Ptychocheilus lucius* appears to take advantage of river transport at the end of the flood period for the dispersal of young from the spawning grounds downstream into productive nursery habitat (Tyus and McAda 1984). This behavior resembles some South American freshwater species in this regard, and it has been noted that in Africa potamodromy may protect the young from predation and secure dispersal over the river basin (Welcomme 1979).

Reproductive Adaptations

The spawning of *P. lucius* occurs in middle to late summer under a decreasing flow regimen. This is unusual among most stream fishes, which spawn in the spring and early summer with rising water levels. As with other potamodromous riverine species, timing of reproduction is very important, and studies of spawning *P. lucius* (Archer et al. 1984) indicate the fish apparently times its spawning to coincide with the descending limb of the hydrograph, a time when downstream transport of young would distribute

them into the shallow nursery habitat that forms during this period in the Green River. Such a temporal adaptation fits in well with the life strategy of *P. lucius*, for the length of exposure of *P. lucius* young to predators is reduced. This reduced time for the young to feed is balanced by delivering them into ideal conditions for growth.

This species selects highly oxygenated white-water rapids and riffles for spawning sites that may be 100 km or more from their preferred adult habitat at that time (Archer and Tyus 1984). Although the mechanism by which these fish congregate in spawning areas is unknown, a homing response (Tyus 1985) could result in sufficient breeding adults returning to a small area to insure good genetic recombination and, therefore, maintain a high degree of genetic diversity in the population.

Natural Adaptations and Controlled Systems

Ptychocheilus lucius evolved as a species adapted to conditions existing at the close of the Cenozoic era. These same adaptations enabled it to compete and survive in the isolated and depauparate Colorado River Basin in the Holocene until the coming of man. Although cause-effect relationships between water development and the decline of the Colorado squawfish have not been proven de facto, it is generally agreed that such development negatively affects the fish (Ono et al. 1983). The life strategies developed from comparing life history attributes of *P. lucius* with late Cenozoic climatic, geologic, and fossil records suggest that evolving life strategies that adapted *P. lucius* to the natural system would ill befit the fish to a controlled system.

Paramount in the life strategy of *P. lucius* is the need for unimpeded movement within the riverine system, and blockage of major stream sections where *P. lucius* occurs has resulted in the extirpation of the fish from these areas (Tyus 1984). In addition, the downstream transport of larva and establishment of shallow euphemeral embayments for nursery areas are needed, and a proper discharge regime must be maintained for spawning and rearing of young.

Life strategies proposed herein for *P. lucius* need refinement and further substantiation. Only by understanding these strategies, however, can we place its evolution in proper context and provide for its future.

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