TABLE 1. List of bird species seen on Cold Spring Mountain and vicinity, northwestern Colorado.

Species	Status: Latilong study[1] (Changes, this study)	Abundance[2]	Dates seen[3]: Earliest	Dates seen[3]: Latest	Nesting dates[4]	Comments
Horned Grebe (*Podiceps auritus*)	M	U		10 Aug[5]		
Eared Grebe (*Podiceps nigricollis*)	B		20 May[5]			
Green-winged Teal (*Anas crecca*)	R	FC	30 Apr	6 Oct	Young:8 Jul	
Mallard (*Anas platrhynchos*)	R	C	31 May	10 Aug		
Northern Pintail (*Anas acuta*)	R	FC	30 Apr	10 Aug		
Blue-winged Teal (*Anas discors*)	B	FC	20 May	8 Jul	Young:8 Jul	
Northern Shoveler (*Anas clypeata*)	R	U	21 May	10 Aug		
American Wigeon (*Anas americana*)	R	FC	8 Jun	25 Aug	Young:8, 15 Jul	
Turkey Vulture (*Cathartes aura*)	B	FC	24 May	27 Sep		
Bald Eagle (*Haliaeetus leucocephalus*)	W	R	5 Apr	7 Nov		
Northern Harrier (*Circus cyaneus*)	R	FC	Seen every month			
Sharp-shinned Hawk (*Accipiter striatus*)	R	U		4, 26 Aug[5]		
Coopers Hawk (*Accipiter cooperii*)	B	U	30 Apr	13 Sep	Nest:30 Apr	
Northern Goshawk (*Accipiter gentilis*)	R(B)	U	30 Apr	19 Sep	Nest:30 Apr	
Swainson's Hawk (*Buteo swainsoni*)	B	FC	16 Aug	27 Sep		
Red-tailed Hawk (*Buteo jamaicensis*)	R	FC	5 Apr	19 Sep		
Ferruginous Hawk (*Buteo regalis*)	B	U	5, 6 Apr[5]			
Rough-legged Hawk (*Buteo lagopus*)	W	C	1 Nov	7 May		
Golden Eagle (*Aquila chrysaetos*)	R	FC	Seen every month		Nest:10 Apr	
American Kestrel (*Falco sparverius*)	R	FC	16 Apr	3 Oct		5 birds feeding on Mormon Crickets on 5 and 6 Aug
Merlin (*Falco columbarius*)	M		20 Aug[5]			
Prairie Falcon (*Falco mexicanus*)	B	FC	4 Apr	27 Jul		
Chukar (*Alectoris chukar*)	R	U	20,24 Jul; 8 Sep[5]			
Blue Grouse (*Dendragapus obscurus*)	R	FC	20 Apr	19 Sep	Young:19 Jul	
Sage Grouse	R	C	Seen every month		Nests:9(2 nests), 19, 20(2), 21, 31(2) May; second nests: 21, 31, May; 5, 17 June; young:many 3-week and older chicks after 12 Jul	
American Coot (*Fulica americana*)	B		30 May[5]			
Sandhill Crane (*Grus canadensis*)	M	R	4,5 Apr[5]			
Killdeer (*Charadrius vociferus*)	R	C	16 Apr	15 Aug	Many juvenile birds: 26–31 Jul	
American Avocet (*Recurvirostra americana*)	B		20 May[5]			
Greater Yellowlegs (*Tringa melanoleuca*)	M			23 Jul[5]		
Lesser Yellowlegs (*Tringa flavipes*)	M			4 Aug[5]		
Solitary Sandpiper (*Tringa solitaria*)	M			22 Jul[5]		
Spotted Sandpiper (*Actitis macularia*)	B	FC	31 May	17 Aug		
Western Sandpiper (*Calidris mauri*)	M	FC		13, 15 Aug[5]		
Long-billed Dowitcher (*Limnodromus scolopaceus*)	M	U		3 Aug[5]		
Common Snipe (*Gallinago gallinago*)	B	FC	26 Apr	23 Jul		
Wilson's Phalarope	b	FC	30 Apr	28 Jul		
Franklin's Gull (*Larus pipixcan*)	M		7 May[5]			
Mourning Dove (*Zenaida macroura*)	R	C	7 May	6 Oct		
Great Horned Owl (*Bubo virginianus*)	R	C	Seen or heard every month			
Northern Pygmy-Owl	(W)		Seen in Irish Canyon on 4 Feb 1984			
Long-eared Owl (*Asio otus*)	R	U	18 Jun	21 Sep		Hendee (1929) found a nest 28 May near the Little Snake River
Common Nighthawk (*Chordeiles minor*)	B	FC	31 May	25 Aug		
Common Poorwill	b(B, Hendee 1929)	FC	14 Jul	19 Sep		Most common second week in Aug; 20–40 birds/night
White-throated Swift	b	U	12 May	26 Sep		
Broad-tailed Hummingbird (*Selasphorus platycercus*)	B	C	3 Jun	26 Aug		
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	M	R	18 Apr	21 May		
Downy Woodpecker	b	FC	12 Apr	19 Sep		
Hairy Woodpecker (*Picoides villosus*)	M	FC	18 Jul	17 Aug		

Table 1 continued.

Species	Status: Latilong study[1] (Changes, this study)	Abundance[2]	Dates seen[3]: Earliest	Dates seen[3]: Latest	Nesting dates[4]	Comments
Three-toed Woodpecker (*Picoides tridactylus*)	(n or b)		Seen on 24 July 1981 at Swede Spring on Cold Spring Mountain			
Northern Flicker (*Colaptes auratus*)	R	C	Seen every month			
Western Wood Pewee	b	FC	8 Jun	10 Aug		
Dusky Flycatcher (*Empidonax oberholseri*)	B	FC	7 Jun	18 Aug		
Gray Flycatcher (*Empidonax wrightii*)	B		3 Jun[5]			
Western Kingbird (*Tyrannus verticalis*)	b	R	8 May	15 Aug		
Horned Lark (*Eremophila alpestris*)	R	C	Seen every month		Nest: 5, 7 Jun	
Tree Swallow (*Tachycineta bicolor*)	B	C	11 Apr	5 Aug		
Violet-green Swallow (*Tachycineta thalassina*)	b(B)	C	21 May	3 Aug	Adult carrying fecal sac:23 Jun	
Barn Swallow (*Hirundo rustica*)	B	FC	15 Apr	5 Aug		
Steller's Jay (*Cyanocitta stelleri*)	R	FC	19 Jul, 13 Sep[5]			
Scrub Jay (*Aphelocoma coerulescens*)	R	FC	Seen every month			
Pinyon Jay (*Gymnorhinus cyanocephalus*)	R	C	Seen every month			More than 50 birds feeding on Mormon Crickets 5 Aug
Clark's Nutcracker (*Nucifraga columbiana*)	R	C	Seen every month			Ten birds feeding on Mormon Crickets 5 Aug
Black-billed Magpie (*Pica pica*)	R	C	Seen every month			More than 100 birds feeding on Mormon Crickets 5 and 17 Aug
American Crow (*Corvus brachyrhynchos*)	R	FC	Seen every month			
Common Raven (*Corvus corax*)	R	FC	Seen every month			
Black-capped Chickadee	W(N)	FC	20 Feb, 14 Apr, 3 May, 15, 17 Aug; 19 Sep[5]			
Mountain Chickadee (*Parus gambeli*)	R	FC	Seen every month			
Plain Titmouse (*Parus inornatus*)	B	FC	3, 4, 8 May[5]			
Bushtit	b		5 May[5]			
Red-breasted Nuthatch (*Sitta canadensis*)	R	U	29 Jun	26 Aug		
White-breasted Nuthatch (*Sitta carolinensis*)	R		21 May[5]			
Rock Wren (*Salpinctes obsoletus*)	B	U	Seen every month			
House Wren (*Troglodytes aedon*)	B	C	4 May	24 Aug	Fledglings:27 Jun	
Ruby-crowned Kinglet (*Regulus calendula*)	M	U	17, 21 May[5]			
Blue-gray Gnatcatcher (*Polioptila caerulea*)	B		15 Jun[5]			
Mountain Bluebird (*Sialia currucoides*)	B	FC	17 Mar	3 Oct		
Townsend's Solitaire (*Myadestes townsendi*)	M	FC	4 May	3 Oct		
American Robin (*Turdus migratorius*)	R	FC	Seen every month at lower elevations		2 nests with 4 eggs:5 Jun	
Northern Mockingbird (*Mimus polyglottos*)	b	UC	6 Jun	3 Oct		
Sage Thrasher (*Oreoscoptes montanus*)	B	FC	6 Apr	25 Aug		
Water Pipit (*Anthus spinoletta*)	(b or M)		3 Oct 1981[5]			4 birds near Arthur's Reservoir
Bohemian Waxwing (*Bombycilla garrulus*)	W		3 Nov[5]			
Northern Shrike (*Lanius excubitor*)	W	U	1, 7 Nov[5]			
Loggerhead Shrike (*Lanius ludovicianus*)	B	U	31 May, 4 Jun[5]			
European Starling (*Sturnus vulgaris*)	R	C	Seen every month			
Warbling Vireo (*Vireo gilvus*)	b(B)	FC	31 May	19 Sep	2 nests:19 Jun	
Yellow Warbler (*Dendroica petechia*)	B	FC	15 Jun	17 Aug		
Yellow-rumped Warbler (*Dendroica coronata*)	B	U	21 May	17 Aug	Adult feeding young: 14 Jul	
Black-throated Gray Warbler (*Dendroica nigrescens*)	B	U	17, 21 May[5]			
MacGillivray's Warbler (*Oporornis tolmiei*)	B	FC	9 Jun	19 Sep		
Common Yellowthroat (*Geothlypis trichas*)	B		15 Jun[5]			
Wilson's Warbler (*Wilsonia pusilla*)	B	FC	17, 18, 25 Aug			
Western Tanager	b	FC	10 Aug[5]			
Black-headed Grosbeak (*Pheucticus melanocephalus*)	B	FC	1 Jun	17 Aug	Female with food: 27 Jul	

Table 1 continued.

Species	Status: Latilong study[1] (Changes, this study)	Abundance[2]	Dates seen[3]: Earliest	Dates seen[3]: Latest	Nesting dates[4]	Comments
Lazuli Bunting (*Passerina amoena*)	b		11 Aug[5]			
Green-tailed Towhee (*Pipilo chlorurus*)	B	FC	4 May	13 Sep	Nest with 4 eggs: 5 Jun; young:20 Jun	
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	B	U	1 May	7 Jun		
American Tree Sparrow (*Spizella arborea*)	W	FC	3 Nov	4 Apr		
Chipping Sparrow (*Spizella passerina*)	B	FC	16 Jun	25 Aug		
Brewer's Sparrow (*Spizella breweri*)	B	C	31 May	19 Sep	Nest:8, 21 Jun; young:23 Jun, 24 Jul	One of the most common breeding species
Vesper Sparrow	b(B)	C	25 Apr	26 Sep	Eggs:21 Jun; fledglings:27 Jun, 23–31 Jul	One of the most common breeding species
Lark Sparrow (*Chondestes grammacus*)	B	FC	8 May	4 Jun		
Sage Sparrow (*Amphispiza belli*)	B	R	3, 6, 30 Apr[5]			
Savannah Sparrow (*Passerculus sandwichensis*)	b		17 Aug[5]			
White-throated Sparrow (*Zonotrichia albicollis*)	M		31 May[5]			
White-crowned Sparrow	M(B)	C	10 May	26 Aug	Nests:1 Jun eggs:1,5 Jun young:15 Aug	Very common breeding species
Dark-eyed Junco (*Junco hyemalis*)	R	FC	Seen every month		Nest:16 Jun young:28 Jun	
Red-winged Blackbird (*Agelaius phoeniceus*)	R	C	20 Apr	19 Sep		
Western Meadowlark (*Sturnella neglecta*)	R	FC	13 Apr	3 Oct		
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	B	FC	2 May	19 Jul		
Brewer's Blackbird (*Euphagus cyanocephalus*)	B	FC	1 May	19 Sep	Nest:19 Jun	More than 100 birds feeding on Mormon Crickets on 6, 18 Aug
Brown-headed Cowbird (*Molothrus ater*)	B	FC	2 May	4 Sep		
Rosy Finch (*Leucosticte arctoa*)	W	U	1 Nov	12 Apr		
Cassin's Finch (*Carpodacus cassinii*)	R	FC	16, 18 May[5]			
Red Crossbill (*Loxia curvirostra*)	b		31 May[5]			
Pine Siskin (*Carduelis pinus*)	W	FC	1 Nov	30 Apr		
American Goldfinch (*Carduelis tristis*)	B		30 May[5]			

[1]Status given in Chase et al. (1982). R = Resident year-round (breeds); N = Nonbreeder present year-round, or a year-round resident whose breeding has not been documented; B = Breeding (documented); b = Likely breeder; W = Winter visitor; M = Migrant; blanks indicate no record.
[2]Abundance categories: C = Common; FC = Fairly common; U = Uncommon; R = Rare; Irr = Irregular. Abundance was estimated in this study, and categories are from Chase et al. (1982). A blank indicate too few data to evaluate.
[3]Dates observed represent our records and may not be indicative of actual arrival/departure dates for migrants and summer residents in the entire region.
[4]Nesting dates are presented only where information is known.
[5]Only date(s) seen.

relatively short because most of these species stop at better habitat in Browns Park; Cold Spring Mountain is mostly xeric, with the exception of six small reservoirs. A notable aspect of the species list is that the breeding status of several relatively common species remains to be documented. Future field workers in this area should attempt to document breeding for Wilson's phalarope (*Phalaropus tricolor*), northern pygmy owl (*Glaucidium gnoma*), common poorwill (*Phalaenoptilus nuttallii*), white-throated swift (*Aeronautes saxatalis*), downy woodpecker (*Picoides pubescens*), western wood pewee (*Contopus sordidulus*), western kingbird (*Tyrannus verticalis*), black-capped chickadee (*Parus atricapillus*), bushtit (*Psaltriparus minimus*), and western tanager (*Piranga ludoviciana*), among others. The northern pygmy owl, three-toed woodpecker, and water pipit were recorded for the first time from this area.

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LITERATURE CITED

BEHLE, W. H., AND J. GHISELIN. 1958. Additional data on the birds of the Uinta Mountains and basin of northeastern Utah. Great Basin Nat. 18: 1–22.

BOCK, C. E. 1984. Geographical correlates of abundance vs. rarity in some North American winter landbirds. Auk 101: 266–273.

CARY, M. 1909. New records and important range extensions of Colorado birds. Auk 26: 180–185.

CHASE, C. A., S. J. BISSELL, H. E. KINGERY, AND W. D. GRAUL. 1982. Colorado bird distribution latilong study. Colorado Field Ornithologists, Denver Mus. Nat. Hist., Denver, Colorado. 78 pp.

HAYWARD, C. 1967. Birds of the upper Colorado River basin. Brigham Young University Sci. Bull., Biol.. Ser. 9(2): 1–64.

HENDEE, R. 1929. Notes on birds observed in Moffat County, Colorado. Condor 31: 24–32.

WALTERS, R. E., AND E. SORENSEN. 1983. Utah bird distribution: latilong study 1983. Utah Dept. Nat. Resour., Div. Wildl. Resour., Nongame Sec., Salt Lake City. 97 pp.

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

Harold M. Tyus[1]

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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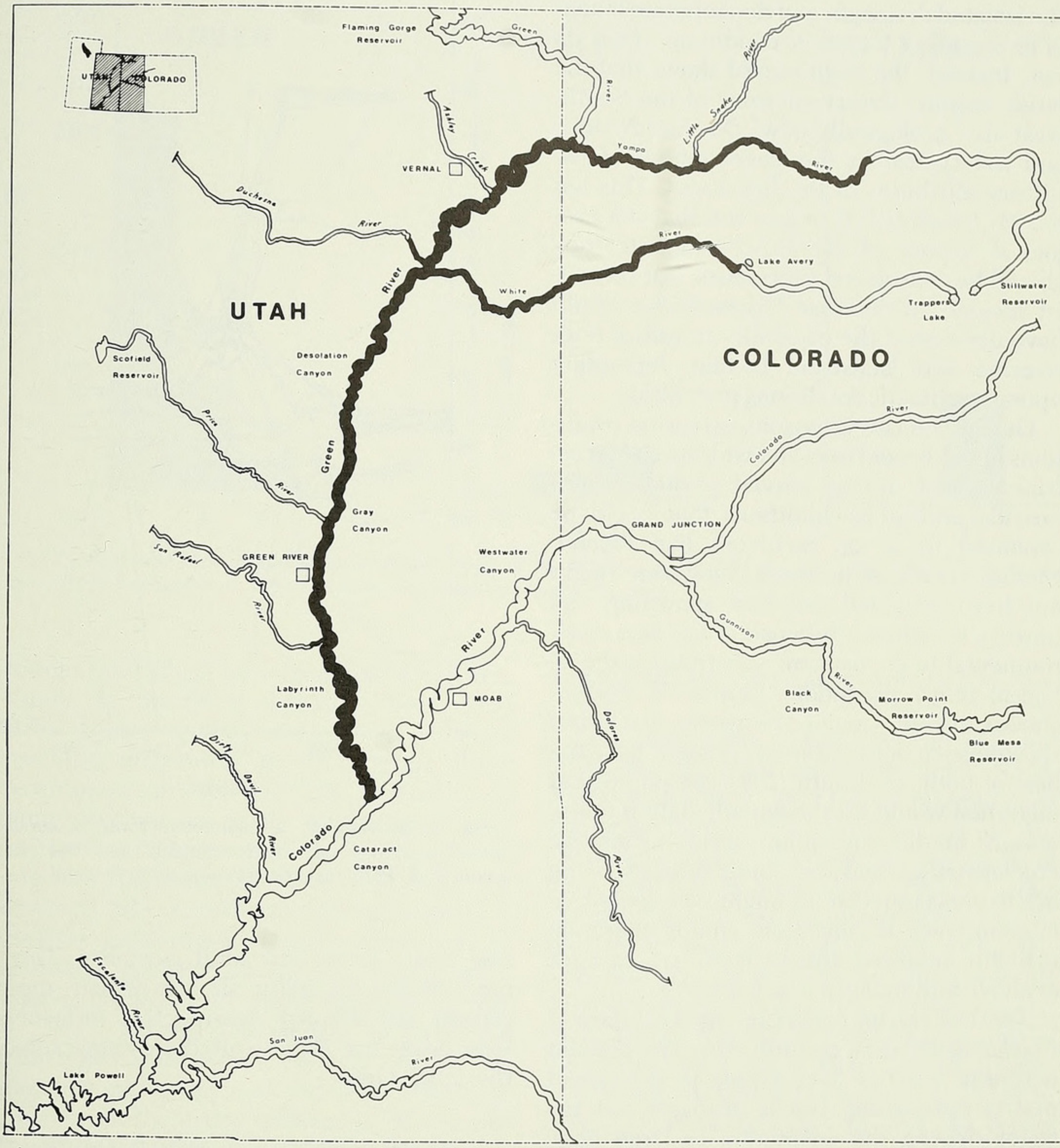

Fig. 1. Upper Colorado River Basin and Green River study area (shaded).

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.

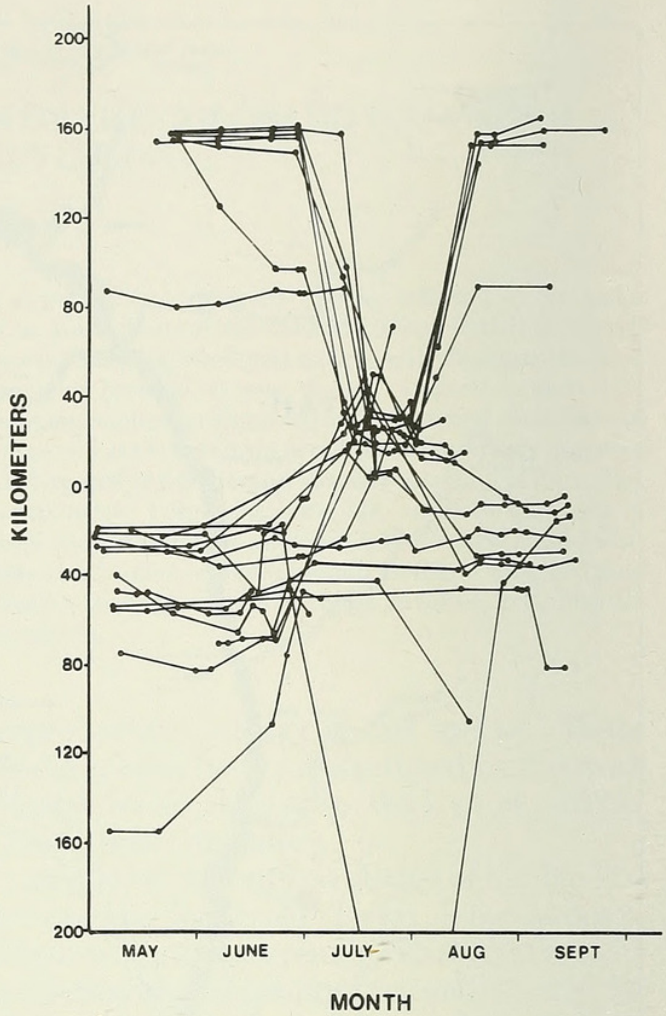

Fig. 2. Movement of radiotelemetered Colorado squawfish, Yampa and Green rivers, 1983 and 1984 (after Archer et al. 1985). Mouth of Yampa River = 0 km.

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

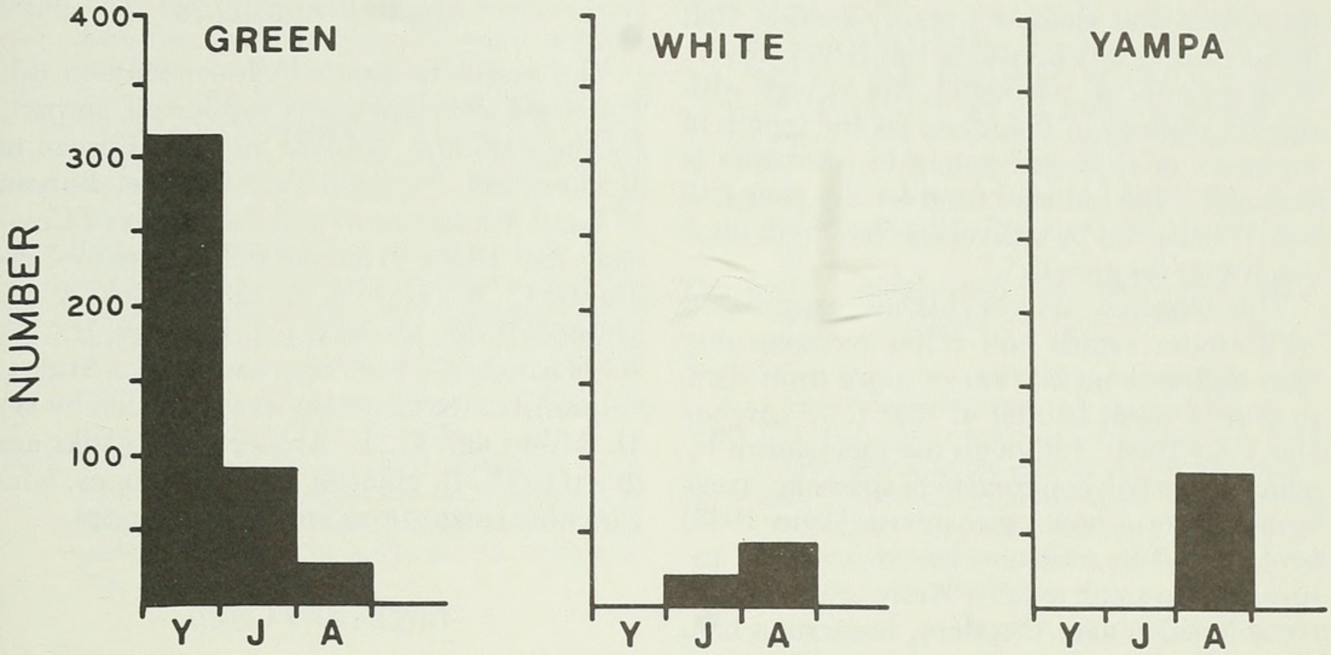

Fig. 3. Catch of Colorado squawfish from the Green, White, and Yampa rivers (Tyus et al. 1982, Miller et al., *White River*, 1982; *Yampa River*, 1982. Y=young of year, J=juveniles, A=adult.

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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Literature Cited

Archer, D. L., and H. M. Tyus. 1984. Colorado squawfish spawning study, Yampa River. U.S. Fish Wildl. Serv., Colorado River Fish. Proj., Salt Lake City, Utah. 34 pp.

Archer, D. L., H. M. Tyus, and L. R. Kaeding. 1985. Colorado River fish monitoring project. Final report. U.S. Fish Wildl. Serv., Colorado River Fish. Proj., Salt Lake City, Utah.

Beckman, W. C. 1952. Guide to the fishes of Colorado. University of Colorado Museum, Boulder, Colorado. 110 pp.

Haynes, C. M., T. A. Lytle, E. J. Wick, and R. T. Muth. 1984. Larval Colorado squawfish (*Ptychocheilus lucius* Girard) in the upper Colorado River Basin, Colorado. 1979–1981. Southwest. Nat. 29: 21–34.

Holden, P. B., and E. J. Wick. 1982. Life history and prospects for recovery of Colorado squawfish. Pages 98–108 *in* W. H. Miller, H. M. Tyus, and C. A. Carlson, eds., Fishes of the upper Colorado River system: present and future. West. Div., Amer. Fish. Soc., Bethesda, Maryland. 131 pp.

Miller, R. R. 1961. Man and the changing fish fauna of the American Southwest. Pap. Mich. Acad. Sci., Arts, Lett. 46: 365–404.

Miller, W. H., D. L. Archer, H. M. Tyus, and K. C. Harper. 1982. White River fishes study. Final report. U.S. Fish Wildl. Serv., Colorado River Fish. Proj., Salt Lake City, Utah.

Miller, W. H., D. L. Archer, H. M. Tyus, and R. M. McNatt. 1982. Yampa River fishes study. Final report. U.S. Fish Wildl. Serv., Colorado River Fish. Proj., Salt Lake City, Utah.

Minckley, W. L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix, Arizona.

Ono, R. P., J. D. Williams, and A. Wagner. 1983. Vanishing fishes of North America. Stone Wall Press, Inc., Washington, D. C. 257 pp.

Smith, G. R. 1981. Effects of habitat size on species richness and adult body sizes of desert fishes. Pages 125–171 *in* R. J. Naiman and D. L. Soltz, eds., Fishes in North American deserts. John Wiley and Sons, New York.

SMITH, M. L. 1975. Fishes of the Pliocene Glenns Ferry formation, southwest Idaho. University of Michigan Papers on Paleontology 14: 1–68.

_____. Late Cenozoic fishes of the warm deserts of North America: a reinterpretation of desert adaptations. Pages 11–38 *in* R. J. Naiman and D. L. Soltz, eds., Fishes in North American deserts. John Wiley and Sons, New York.

TYUS, H. M. 1984. Loss of stream passage as a factor in the decline of the endangered Colorado squawfish. Pages 138–144 *in* Issues and technology in the management of impacted western wildlife. Tech. Pub. 14, Thorne Ecol. Inst., Boulder, Colorado.

_____. 1985. Homing behavior noted for Colorado squawfish. Copeia 1985: 213–215.

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. Southwest. Nat. 29: 289–299.

TYUS, H. M., C. W. MCADA, AND B. D. BURDICK. 1982. Green River fishery investigations: 1979–1981. Pages 1-99 *in* Final report of the U.S. Fish and Wildlife Service and U.S. Bureau of Reclamation, Part 2. U.S. Fish Wildl. Serv., Colorado River Fish. Proj., Salt Lake City, Utah.

U.S. FISH AND WILDLIFE SERVICE. 1973. Threatened wildlife of the U.S. Resource Publ. 114. Washington, D. C.

_____. 1974. Colorado squawfish: determination as an endangered species. Fed. Reg. 45(80): 27710–27713.

WELCOMME, R. L. 1979. Fisheries ecology of floodplain rivers. Longman Group Ltd. London. 296 pp.

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. Technical Report 83-7, Water Resources Laboratory, Natl. Park Serv., Fort Collins, Colorado. 55 pp.

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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Literature Cited

ARCHER, D. L., AND H. M. TYUS. 1984. Colorado squawfish spawning study, Yampa River. U.S. Fish Wildl. Serv., Colorado River Fish. Proj., Salt Lake City, Utah. 34 pp.

ARCHER, D. L., H. M. TYUS, AND L. R. KAEDING. 1985. Colorado River fish monitoring project. Final report. U.S. Fish Wildl. Serv., Colorado River Fish. Proj., Salt Lake City, Utah.

BECKMAN, W. C. 1952. Guide to the fishes of Colorado. University of Colorado Museum, Boulder, Colorado. 110 pp.

HAYNES, C. M., T. A. LYTLE, E. J. WICK, AND R. T. MUTH. 1984. Larval Colorado squawfish (*Ptychocheilus lucius* Girard) in the upper Colorado River Basin, Colorado. 1979–1981. Southwest. Nat. 29: 21–34.

HOLDEN, P. B., AND E. J. WICK. 1982. Life history and prospects for recovery of Colorado squawfish. Pages 98–108 *in* W. H. Miller, H. M. Tyus, and C. A. Carlson, eds., Fishes of the upper Colorado River system: present and future. West. Div., Amer. Fish. Soc., Bethesda, Maryland. 131 pp.

MILLER, R. R. 1961. Man and the changing fish fauna of the American Southwest. Pap. Mich. Acad. Sci., Arts, Lett. 46: 365–404.

MILLER, W. H., D. L. ARCHER, H. M. TYUS, AND K. C. HARPER. 1982. White River fishes study. Final report. U.S. Fish Wildl. Serv., Colorado River Fish. Proj., Salt Lake City, Utah.

MILLER, W. H., D. L. ARCHER, H. M. TYUS, AND R. M. MCNATT. 1982. Yampa River fishes study. Final report. U.S. Fish Wildl. Serv., Colorado River Fish. Proj., Salt Lake City, Utah.

MINCKLEY, W. L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix, Arizona.

ONO, R. P., J. D. WILLIAMS, AND A. WAGNER. 1983. Vanishing fishes of North America. Stone Wall Press, Inc., Washington, D. C. 257 pp.

SMITH, G. R. 1981. Effects of habitat size on species richness and adult body sizes of desert fishes. Pages 125–171 *in* R. J. Naiman and D. L. Soltz, eds., Fishes in North American deserts. John Wiley and Sons, New York.

SMITH, M. L. 1975. Fishes of the Pliocene Glenns Ferry formation, southwest Idaho. University of Michigan Papers on Paleontology 14: 1–68.

_____. Late Cenozoic fishes of the warm deserts of North America: a reinterpretation of desert adaptations. Pages 11–38 *in* R. J. Naiman and D. L. Soltz, eds., Fishes in North American deserts. John Wiley and Sons, New York.

TYUS, H. M. 1984. Loss of stream passage as a factor in the decline of the endangered Colorado squawfish. Pages 138–144 *in* Issues and technology in the management of impacted western wildlife. Tech. Pub. 14, Thorne Ecol. Inst., Boulder, Colorado.

_____. 1985. Homing behavior noted for Colorado squawfish. Copeia 1985: 213–215.

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. Southwest. Nat. 29: 289–299.

TYUS, H. M., C. W. MCADA, AND B. D. BURDICK. 1982. Green River fishery investigations: 1979–1981. Pages 1-99 *in* Final report of the U.S. Fish and Wildlife Service and U.S. Bureau of Reclamation, Part 2. U.S. Fish Wildl. Serv., Colorado River Fish. Proj., Salt Lake City, Utah.

U.S. FISH AND WILDLIFE SERVICE. 1973. Threatened wildlife of the U.S. Resource Publ. 114. Washington, D. C.

_____. 1974. Colorado squawfish: determination as an endangered species. Fed. Reg. 45(80): 27710–27713.

WELCOMME, R. L. 1979. Fisheries ecology of floodplain rivers. Longman Group Ltd. London. 296 pp.

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. Technical Report 83-7, Water Resources Laboratory, Natl. Park Serv., Fort Collins, Colorado. 55 pp.

PARASITES OF THE WOUNDFIN MINNOW, *PLAGOPTERUS ARGENTISSIMUS*, AND OTHER ENDEMIC FISHES FROM THE VIRGIN RIVER, UTAH

Richard A. Heckmann[1], James E. Deacon[2], and Paul D. Greger[2]

ABSTRACT.—Two hundred woundfin minnows, *Plagopterus argentissimus*, from four sites along the Virgin River, Utah, were examined on two dates during summer 1985. The foreguts of 211 woundfin and variable numbers of other fishes from the Virgin River near Beaver Dam Wash, Arizona, and Mesquite, Nevada, were examined for cestodes on four dates throughout 1979. Seven parasites were found in *P. argentissimus: Posthodiplostomum minimum* (metacercariae), *Diplostomum spathaceum* (metacercariae), *Bothriocephalus acheilognathi*, *Gyrodactylus* sp., *Lernaea cyprinacea*, *Trichodina* sp., and *Ichthyophythirius multifiliis*. Fungal infections were noted on two fish during the study. Seventeen Virgin River roundtail chub, *Gila robusta seminuda*, were examined from two of the four sites in 1985 and 64 specimens from Beaver Dam Wash were examined in 1979. *Gila robusta seminuda* was infected with *Posthodiplostomum minimum* (metacercariae) and *Bothriocephalus acheilognathi*, the Asian fish tapeworm. This cestode probably gained entrance into the ichthyofauna of the Virgin River from red shiners, *Notropis lutrensis*, and has the potential of being very detrimental to the endemic and endangered fishes of the Virgin River. Parasite loads were correlated with water quality and habitat disturbance, with highest number and frequency occurring in "disturbed" sites. Low river flows and increased total dissolved solids appear to be associated with a higher parasite frequency and mean number in fishes of the Virgin River. These data represent the first known published records for parasites of the woundfin minnow and Virgin River roundtail chub.

There is a paucity of information on the parasitofauna of the woundfin minnow, *Plagopterus argentissimus*, and other species of fish from the Virgin River, Utah-Arizona-Nevada. Many of the fishes in the Virgin River are endemic and have been listed as endangered species, the woundfin included. Hoffman (1967) lists no parasites for the woundfin. Other common fishes in the Virgin River drainage include the Virgin roundtail chub, *Gila robusta seminuda;* speckled dace, *Rhinichthys osculus;* Virgin spinedace, *Lepidomeda mollispinis;* desert sucker, *Catostomus clarki;* flannelmouth sucker, *Catostomus latipinnis;* and the introduced red shiner, *Notropis lutrensis*. Parasites of these later species are also poorly known (Hoffman 1967). Parasites can have adverse effects on fish populations. Changes in incidence, intensity, or parasite species infecting or infesting a host can provide important clues to the health and status of fish host populations. To understand management options, it is essential to also know the life cycle of the parasite and its effects at various levels of infection. For example, parasitism can be responsible for reduced growth rates, reduced egg production, poor swimming performance, aberrant behavior, etc. (David 1947, Dogiel 1958, Hoffman 1967).

The primary objectives of this study were as follows:

1. Identify the species of parasites inhabiting the woundfin minnow at selected sites in the Virgin River in Utah.
2. Determine the frequency of occurrence, abundance, and temporal variation of parasites for *P. argentissimus* in the summer during the normal period of low flow.
3. Determine the relationship between parasitism and the immediate habitat of the host.
4. Determine the pathogenicity of the parasite to the host.

In a previous study conducted during 1979 (Greger 1983), woundfin minnows examined during February and June near Beaver Dam Wash, Arizona, were not parasitized by cestodes. Cestodes were present, however, in the foreguts of *P. argentissimus* and increased in both number and frequency from September to December. Frequency of infection of woundfin with cestodes was much less near Beaver Dam Wash, Arizona, than was true further downstream in Nevada. This suggested that woundfin may be more vulnerable to parasitism in an agriculturally disturbed habitat than in a more natural environment. Because the Virgin River near St. George,

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Utah, exhibits similar agricultural disturbances, our hypothesis was that the parasite load in the fish population near St. George would be higher than in the less disturbed sections of Virgin River in Utah.

The life cycles of cestodes and other parasites of fishes from the Virgin River have not been determined in detail. In general, fishes can be both definitive and intermediate hosts for cestodes. Reproductively mature adult cestodes present in fish will release eggs from gravid proglottids while in the intestine of the host. The eggs passs through the host's anus and may settle in the stream sediments. For many cestodes, increasing temperature causes the operculate eggs to hatch, releasing a ciliated coracidium (motile oncosphere). Cyclopoid copepods (first intermediate host) ingest these larvae and become infected. The oncosphere sheds its ciliated coat in the gut of the copepod and burrows through the intestinal wall to the hemocoel, where it develops into a procercoid larvae (Cheng 1973). This mesacestode-type larva cannot become infective to a definitive host for about two to three weeks, until cercomer formation (Cheng 1973). If a fish ingests an infected copepod, the adult cestode may commence development in the intestine of the host. Although larval (pleroceroid) development in a second intermediate host (such as a smaller fish) is possible, it is unlikely to occur in the Virgin River ichthyofauna, since no primarily piscivorous fishes are present. It seems more probable that development of the adult cestode in Virgin River fishes occurs following ingestion of an infected copepod. Direct development of the adult pseudophyllidean cestode *Eubothrium salvelini* following ingestion of infected *Cyclops* sp. by Sockeye salmon, *Oncorhynchus nerka*, has been reported by Smith (1973) from a lake in British Columbia.

The effects of adult cestodes upon fish hosts have not been studied in detail. Rees (1967), after an extensive review of the literature, reached no definitie conclusions regarding the lethal effects of adult cestodes. Other investigators have suggested that adverse effects are considerable. Smith (1973) reported that noninfected salmon smolts grew 5%–7% longer and 17%–24% heavier than infected smolts. Field observations and swimming performance tests suggested cases of reduced swimming abilities and earlier fatigue in salmon and trout infected with helminths (Smith and Margolis 1970, Heckman 1983). These data also demonstrate some nutritional or growth impairments for infected fish. Other researchers (Wardle 1933, Dogiel 1958, Dombroski 1955) have reported that adult pseudophyllidean cestodes can affect host nutrition and survival. Severe occlusion (impaction) of the gut has been reported for infected salmon (Dogiel 1964) and appeared to affect the nutritional status in severe cases. Impaction by parasites would also affect reproductive potential. Williams and Halvorsen (1971) negated the belief that contents of the fish host intestine represent an unlimited source of food for cestodes. Impaction and reduced growth and vigor would also reduce reproductive potential.

Other indirect effects of cestode adults on their hosts have been demonstrated in the laboratory. Boyce and Clarke (1983) determined that Sockeye salmon yearlings infected with tapeworms had a reduced ability to adapt to seawater as evidenced by increased mortality and elevated plasma sodium levels. Boyce and Behrens-Yamada (1977) also reported Sockeye salmon juveniles infected with the same cestode, *Eubothrium salvelini*, to be more sensitive to zinc toxicity. These effects could make the infected fish less vigorous and more susceptible to predation during its seaward migration.

The Asian fish tapeworm, *Bothriocephalus acheilognathi*, introduced into this country by imports of grass carp, has been described as a dangerous parasite in Europe (Bauer et al. 1981). This cestode has apparently become established in the ichthyofauna of southern Utah.

The most common fish parasite found in this survey was the metacercarial state of the digenetic trematode, *Posthodiplostomum minimum*. "Black spot," for example, is caused by metacercarie found in melanin-pigmented cysts in the skin. This larval stage of flukes may be found in all tissues of fish (Spall and Summerfelt 1969b).

MATERIALS AND METHODS

The 1979 collections were made in February, June, September, and December near Beaver Dan Wash, Arizona, and Mesquite, Nevada (Fig. 1). At each location, the foregut

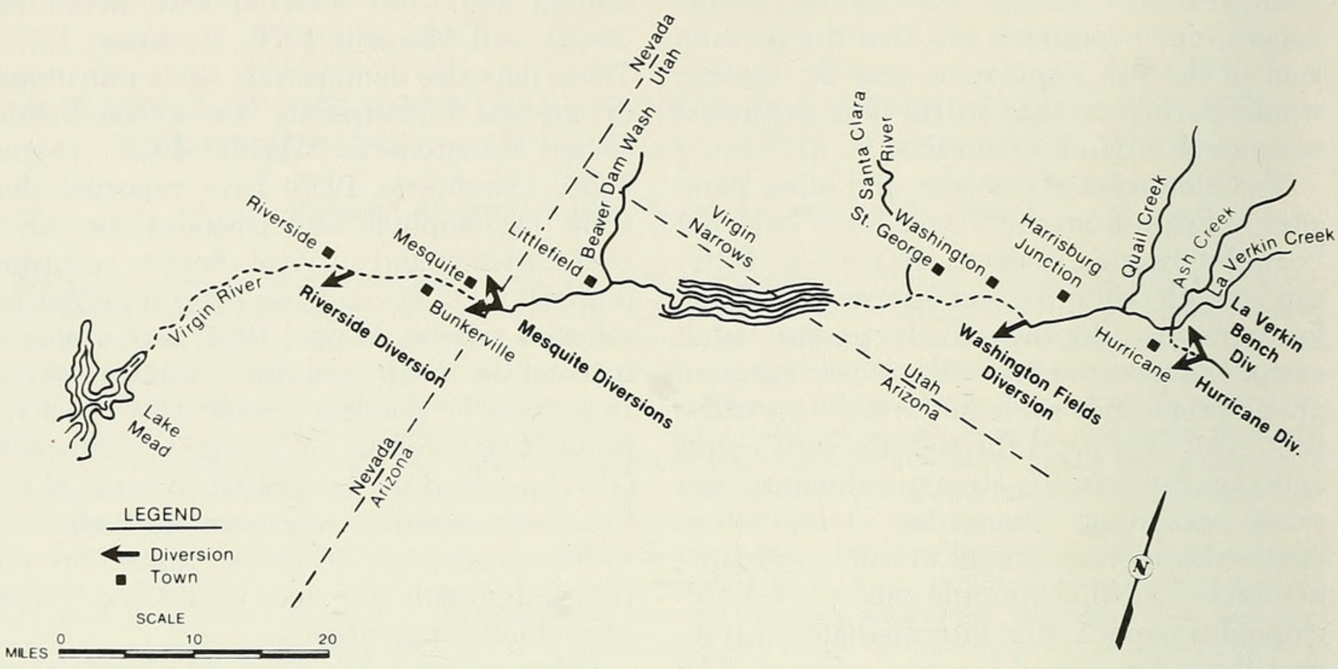

Fig. 1. Fish sampling sites along the Virgin River, Utah, Nevada, Arizona, for this study.

TABLE 1. Rating scale to indicate approximate density of the metacercarial infection in Virgin River fishes.

Assigned scale number	Average number of metacercariae per microscopic field at 20X
0	None
1	1–9
2	10–19
3	20–29
4	30–39
5	40–TNTC

of 22–34 woundfin and variable numbers of other species was examined. Because the 1979 study was conducted as a part of a study of food habits (Greger 1983), we looked only for cestodes in the foregut.

The 1985 collections were taken from the Virgin River on 27 and 28 July and 23, 24, 25, and 31 August 1985. Collections were made about 1/4 mile downstream from the inflow of the Santa Clara River, at Twin Bridges, about two miles below Berry Springs, and at Hurricane Bridge in Utah, and downstream in Nevada near Mesquite (Fig. 1). At each location 23–25 *P. argentissimus* and variable numbers of other fish species were examined. At Mesquite we examined 88 red shiners.

In 1985 external examination for parasitism was made immediately following death of the fish. Scrapings of mucus and epithelial cells were taken from the gill surface, the base of the fins, and the lateral surface of the body. Scrapings were mixed in physiological saline and examined at 100X and 430X. Blood samples were obtained from peripheral circulation on microscope slides, air dried, and later stained (Giemsa-Wright combination) prior to examination at 430X and 1000X. Each blood slide was examined for a minimum of 10 minutes.

The abdominal cavity was opened ventrally and internal organs were examined. Each organ was removed and placed in a saline solution prior to examination with a dissecting microscope. Eye tissues, including the lens, were also examined.

Cestodes were excised from the intestinal tract, enumerated and fixed in AFA. Some individual worms were prepared for examination by scanning electron microscopy by fixation in 3% gluteraldehyde with an acrolein buffer.

Viscera and gills from two woundfin from each of the four sampling locations were fixed in buffered 10% formalin and prepared for tissue evaluation at the Brigham Young University laboratory. These samples were processed by standard methods, stained, and examined closely to evaluate parasite pathology. Two stains, trichrome, and hematoxylin and eosin were used for the tissue sections.

During the first day of study it was noted that many fish were heavily parasitized by metacercariae of the trematode, *Postho-*