[1889]

23.—THE FISHES OF THE COLORADO BASIN.

By BARTON W. EVERMANN AND CLOUD. RUTTER.

In this paper we have attempted to indicate in succinct form our present knowledge of the geographic distribution of the fishes in the basin of the Colorado River of the West. The approximate area drained by the Colorado and its tributary streams is 225,049 square miles. This embraces all of the Territory of Arizona, a narrow strip along the entire length of the western side of New Mexico, a large part of western Colorado, a portion of southwestern Wyoming, nearly all of the eastern half of Utah and a narrow strip in the southwestern part of that Territory, and a small portion of the comparatively arid region of southeastern California.

The Colorado is more than 1,200 miles in length, and is, next to the Columbia, the greatest river of our Western States. It has its rise in the Wind River Mountains of western Wyoming, near the headwaters of four other great rivers, the North Platte, the Big Horn, the Yellowstone, and the Snake, and flows southward through Wyoming into Utah, just touching the northwest corner of Colorado. Until joined by the Grand River in Utah, in about latitude 40° 20′, it is known as the Green River. The area drained by the Green River is about 47,222 square miles. Near the middle of the south line of Utah the Colorado passes into Arizona, then, flowing westward through the Grand Canyon, reaches the Nevada line. After receiving the Rio Virgen from the north, the Colorado turns abruptly southward and pursues this general direction until it reaches the Gulf of California, into which it flows about 50 miles south of the international boundary. It forms over two-thirds of the boundary line between Arizona and Nevada, and all of that between Arizona and California.

The following is a classified list of the rivers and more important creeks of the Colorado Basin. Those in which collecting has been done are printed in italics:

- *Colorado River:*
  - *Gila River.*
    - *Santa Cruz River.*
    - *San Pedro River.*
      - Babacomari River.
    - *Salt River.*
      - *White Mountain Creek.*
    - Aqua Frio Creek.
  - Cataract Creek.
  - Little Colorado River.
    - *Zuñi River.*
  - San Juan River.
    - *Rio de las Animas Perdidas.*
      - *Mineral Creek.*
      - *Leiter Creek.*
      - *Rio Florida.*
      - *Rio de las Piedras.*
    - *Pagosa Springs.*

- *Colorado River*—Continued.
  - Grande River.
    - *Gunnison River.*
      - *Uncompahgre River.*
    - *Cimarron Creek.*
      - *Tomichi Creek.*
    - *Sweetwater Lakes.*
    - *Trapper Lake.*
    - *Eagle River.*
    - *Roaring Fork.*
    - *Cañon Creek.*
  - *Green River.*
    - White River.
    - Yampa River.
      - Little Snake River.
    - Duchesne River.
    - San Rafael River.
    - Dirty Devil River.
    - *Price River.*
    - *Virgen River.*

The principal tributaries from the east are the Rio Gila (draining 68,623 square miles) and the Little Colorado or Colorado Chiquito (draining 29,268 square miles), in Arizona; the San Juan in New Mexico, Colorado, and Utah (draining 26,472 square miles); the Grand, White, and Yampa in Colorado, and the Big Sandy River in Wyoming. The streams from the west are few and rather small, the Duchesne, Price, and Virgen being the only ones of any importance. The tributaries from Colorado are all clear, cold, mountain streams well suited to trout; the headwaters of Green River are similar in character; while the tributaries from Utah, Nevada, California, and Arizona are from comparatively arid regions. During time of rains these streams become of considerable size and are very turbid from the easily eroded country through which they flow. They decrease in size as readily, and in some cases disappear in the sand. Such streams are of course unsuited to a large variety of fish life.

While the headwaters of the Colorado are ordinarily clear and pure, the lower Colorado is one of the muddiest rivers in America and is unfit for any but mud-loving species. As already pointed out by Dr. Jordan,* the headwaters are well supplied with trout, accompanied by *Agosia yarrowi* and the blob (*Cottus bairdi punctulatus*). Lower down appear four species of suckers (*Xyrauchen cypho*, *X. uncompahgre*, *Catostomus latipinnis*, and *Pantosteus delphinus*), and with them the round-tail (*Gila robusta*), the "white salmon" (*Ptychocheilus lucius*), and Williamson's whitefish (*Coregonus williamsoni*). Still lower down are found the bony-tail (*Gila elegans*) and other species of *Catostomus*, while in the Arizona region and the other arid portions are found the peculiar genera *Lepidomeda*, *Meda*, and *Plagopterus*.

Very little collecting has been done in the Colorado Basin, the following being a list of all the collections, or at least all those which have been reported upon and the literature of which is accessible to us:

1. Three nominal species collected by Dr. S. W. Woodhouse, naturalist to Capt. Sitgreaves's expedition, 1852. These were described by Baird & Girard in 1853.

2. Eighteen nominal species collected by the naturalists of the Pacific Railroad Survey and of the United States and Mexican Boundary Survey (John H. Clark, John L. Le Conte, Arthur Schott, Dr. C. B. Kennerly, and Dr. A. L. Heermann). These constituted the first considerable collections, and were described by Baird & Girard, or Girard alone, in 1853–56.

3. Thirteen nominal species obtained by Campbell Carrington, naturalist to the Hayden surveys of 1870 and 1871. These collections were studied and reported upon by Prof. Cope, in 1871 and 1872.

4. Twenty-seven nominal species collected by the various naturalists of the Wheeler Survey (Cope, Yarrow, Henshaw, Newberry, Klett, Rothrock, Rutter, Loew, Bischoff, and Birnie) in 1871–74. These are by far the most extensive collections which have as yet been made in this region, and formed the basis for the admirable report by Cope & Yarrow in volume 5 of the Wheeler Reports and for Prof. Cope's valuable paper on the Plagopterinæ and the Ichthyology of Utah, in 1874.

5. One species (*Xyrauchen cypho*) obtained at the mouth of the Gila, and described by Mr. William N. Lockington in 1880.

6. Seven nominal species collected at Fort Thomas, Ariz., by Lieut. W. L. Carpenter, U. S. A. These were reported upon by Philip H. Kirsch in 1889.

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*Bull. U. S. Fish Commission, IX, 1889 (1891), 22.

7. Eleven nominal species collected in Colorado and Utah in 1889 by Dr. David S. Jordan, Prof. Barton W. Evermann, Mr. Bert Fesler, and Mr. Bradley M. Davis. These were reported upon by Dr. Jordan in 1890.

8. One species (*Gila robusta*) collected in Babacomari Creek near Fort Huachuca, Ariz., in May, 1892, by Dr. A. K. Fisher, to whom we are indebted for the privilege of examining these and other fishes collected by him.

9. Seven species obtained by the present writers from Green River at Green River, Wyo., in 1893. The report upon these species is contained in this paper.

10. Collections have recently been made at Yuma and elsewhere in Arizona by Dr. Charles H. Gilbert, but other than describing one new species he has not yet published the results.

The fish fauna of the Colorado Basin is not rich in number of species, the total number now recognized being but 32 native species. These represent 5 families and 18 genera, as follows:

Catostomidæ, 8 species: *Pantosteus*, 3; *Catostomus*, 3; *Xyrauchen*, 2.
Cyprinidæ, 19 species: *Ptychocheilus*, 1; *Gila*, 3; *Leuciscus*, 4; *Tiaroga*, 1; *Rhinichthys*, 1; *Agosia*, 4; *Couesius*, 1; *Lepidomeda*, 2; *Meda*, 1; *Plagopterus*, 1.
Salmonidæ, 2 species: *Salmo*, 1; *Coregonus*, 1.
Pœciliidæ, 2: *Cyprinodon*, 1; *Heterandria*, 1.
Cottidæ, 1: *Cottus*, 1.

Though the families and species constituting the fish fauna are very few, they are of unusual interest to the student of geographic distribution.

The Cyprinidæ, or minnow family, is by far the most important family as to the number of species, embracing as it does almost 60 per cent of the entire number. The Catostomidæ, or sucker family, comes next, with 8 species, or 25 per cent of the total number. Of the 18 genera, *Xyrauchen*, *Gila*, *Tiaroga*, *Meda*, and *Plagopterus* are thus far known only from the Colorado Basin; *Lepidomeda* was not known to occur elsewhere, until recently discovered by Dr. Gilbert among the fishes collected in the Great Basin in southwestern Nevada by the Death Valley expedition; *Ptychocheilus* is a Pacific Coast genus, represented in most of the larger streams of California, Oregon, and Washington; *Pantosteus*, *Agosia*, and *Heterandria*, as now limited, are genera of rather wide distribution in the western part of the United States; while the 8 remaining genera are found throughout middle North America.

Of the 32 species, all but 7 are thus far known only from this basin. The 7 species which are not confined to the Colorado Basin are the Utah chub (*Leuciscus lineatus*), the western dace (*Rhinichthys cataractæ dulcis*), *Agosia chrysogaster*, Williamson's whitefish, the blob, *Lepidomeda vittata*, and *Girardinus macularius*. The home of the Utah chub is in the Utah and Upper Snake River basins. The western dace belongs in the headwaters of the Missouri, Platte, Arkansas, and Rio Grande, and in the Utah and Columbia basins. Williamson's whitefish and the blob occur in the headwaters of all of our western rivers. *Lepidomeda vittata*, the fifth species, has been taken only once outside of the Colorado Basin. It is thus seen that over 78 per cent of the species of fishes now known from the Colorado Basin are peculiar to it. This is a larger percentage of species peculiar to a single river basin than is found elsewhere in North America.

BIBLIOGRAPHY OF THE ICHTHYOLOGY OF THE COLORADO BASIN.

We here give, in chronological order, the titles of the papers which contain information regarding the fishes of the Colorado Basin, with the place of publication and a brief summary of contents. In the tables of species we give the page upon which each species is mentioned, the name under which recorded, and our identification of each. Genera and species described as new are printed in italics.

1848. LIEUT. COL. W. H. EMORY. Notes of a military reconnoissance from Fort Leavenworth, in Missouri, to San Diego, in California, including part of the Arkansas, Del Norte, and Gila Rivers. By Lieut. Col. W. H. Emory, made in 1846-47, with the advanced guard of the "Army of the West." Washington: Wendell and Van Benthuysen, Printers. 1848.

This interesting volume, which was printed as Ex. Doc. No. 41, Thirteenth Congress, first session, contains the first reference which we have been able to find to any fish of the Colorado Basin. The reference is contained in the following extract from pp. 62 and 63, and is accompanied by a full-page plate of the fish named Gila trout, which, of course, is *Ptychocheilus lucius:*

> A good road was subsequently found turning the spur and following the creek, until it debouched into the Gila, which was only a mile distant. Some hundred yards before reaching this river the roar of its waters made us understand that we were to see something different from the Del Norte. Its section, where we struck it (see the map), 4,347 feet above the sea, was 50 feet wide and an average of 2 feet deep. Clear and swift it came bouncing from the great mountains which appeared to the north about 60 miles distant. We crossed the river, its large round pebbles and swift current causing the mules to tread warily. We followed its course, and encamped under a high range of symmetrically formed hills overhanging the river. Our camp resembled very much the center of a yard of huge stacks.
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> We heard the fish playing in the water, and soon those who were disengaged were after them. At first it was supposed they were the mountain trout, but, being comparatively fresh from the hills of Maine, I soon saw the difference. The shape, general appearance, and the color are the same; at a little distance you will imagine the fish covered with delicate scales, but on a closer examination you will find that they are only the impression of scales. The meat is soft, something between the trout and the catfish, but more like the latter. They are in great abundance.

1853*a*. S. F. BAIRD AND CHARLES GIRARD. Descriptions of some new Fishes from the River Zuñi. <Proc. Ac. Nat. Sci. Phila., VI, 1853, 368, 369.

In this short paper are described and named the first species of fishes ever received from the Colorado Basin. Excepting the brief reference in Lieut. Col. Emory's reconnoissance, which we have quoted above, this is the first mention of Colorado Basin fishes. The specimens described were collected by Dr. S. W. Woodhouse while attached as surgeon and naturalist to the expedition of Capt. Sitgreaves, for the exploration of the Zuñi River and its tributaries. Three species were described from this collection, viz: *Gila robusta*, *Gila elegans*, and *Gila gracilis*. The last of these is now regarded as a synonym of *G. robusta*.

1853*b*. SPENCER F. BAIRD AND CHARLES GIRARD. Fishes collected by the expedition of Capt. L. Sitgreaves, 148-152, with 3 plates, 1853. <Report of an Expedition down the Zuñi and Colorado Rivers, by Captain L. Sitgreaves, Corps Topographical Engineers, 1853.

This paper was based upon the material upon which the same authors reported in the Proceedings of the Philadelphia Academy in 1853. This report, however, is given more in detail and is accompanied by 3 plates containing very good figures of the 3 nominal species—*Gila robusta*, *Gila elegans*, and *Gila gracilis*. This expedition left Zuñi September 24, 1852, and reached Yuma November 30.

1853c. SPENCER F. BAIRD AND CHARLES GIRARD. Descriptions of New Species of Fishes collected by Mr. John H. Clark, on the U. S. and Mexican Boundary Survey, under Lt. Col. Jas. D. Graham. <Proc. Ac. Nat. Sci. Phila., VI, 1853, 387–390.

This is the first of the several papers based upon the collections made by the parties of the Mexican Boundary Survey proper. In it are mentioned 17 species, all of which are described as new. One of these (*Fundulus tenellus=Zygonectes notatus*) is described from Prairie Mer Rouge, La., and Russellville, Ky., 11 from Texas, and 5 from the Colorado Basin.

Page.	Species as recorded.	Present identification.	Page.	Species as recorded.	Present identification.
388	Catostomus *latipinnis*	Catostomus latipinnis.	389	Cyprinodon *macularius*	Cyprinodon macularius.
388	Gila *emoryi*	Gila elegans.	390	Heterandria *occidentalis*	Heterandria occidentalis.
389	Gila *grahami*	Gila robusta.			

1854. S. F. BAIRD AND CHARLES GIRARD. Descriptions of new species of Fishes collected in Texas, New Mexico, and Sonora, by Mr. John H. Clark, on the U. S. and Mexican Boundary Survey, and in Texas by Capt. Stewart Van Vliet, U. S. A. Second Part. <Proc. Ac. Nat. Sci. Phila., VII, 1854, 24–29.

This is the second paper by Baird & Girard upon the fishes of the Mexican Boundary Survey. The list contains 19 species, all but 2 of which are described as new. Of these 19 species, 16 were from Texan waters and 3* from the Colorado Basin.

Page.	Species as recorded.	Present identification.	Page.	Species as recorded.	Present identification.
27	Catostomus *clarkii*	Catostomus clarkii.	204	Tiaroga *cobitis*	Tiaroga cobitis.
28	Catostomus *insignis*	Catostomus insignis.	205	Gila robusta	Gila robusta.
28	Gila *gibbosa*	Leuciscus niger.	205	Gila elegans	Gila elegans.

1856. CHARLES GIRARD. Researches upon the Cyprinoid Fishes inhabiting the fresh waters of the United States of America, west of the Mississippi Valley, from specimens in the Museum of the Smithsonian Institution. <Proc. Ac. Nat. Sci. Phila. 1856, 165–209.

This paper mentions 18 species from the Colorado Basin, 9 of which are described as new.

Page.	Species as recorded.	Present identification.	Page.	Species as recorded.	Present identification.
173	Minomus insignis	Catostomus insignis.	205	Gila gracilis	Gila robusta.
173	Minomus clarkii	Catostomus clarkii.	205	Gila grahamii	Gila robusta.
173	Acomus latipinnis	Catostomus latipinnis.	205	Gila emorii	Gila elegans.
186	Argyreus *osculus*	Agosia oscula.	206	Tigoma *intermedia*	Leuciscus intermedius.
186	Argyreus *notabilis*	Agosia oscula.	207	Tigoma gibbosa	Leuciscus niger.
187	Agosia *chrysoga[s]ter*	Agosia chrysogaster.	209	Ptychocheilus *lucius*	Ptychocheilus lucius.
187	Agosia *metallica*	Agosia chrysogaster.	209	Ptychocheilus *vorax*	Gila robusta.
192	Meda *fulgida*	Meda fulgida.			

1858. CHARLES GIRARD. Report upon the Fishes collected by the various Pacific Railroad Explorations and Surveys. Vol. X, part IV, 1–400, with numerous plates.

But little collecting in the Colorado Basin was done by the parties connected with the Pacific railroad surveys. The records mention only three species from this basin. All of these were collected in the Zuñi River in 1852 by Dr. S. W. Woodhouse, under Capt. L. Sitgreaves. Specimens of one of the species (*Gila elegans*) were obtained in the Gila in 1853 by Dr. A. L. Heermann, under Lieut. J. G. Parke; in the Colorado River in 1854 by Arthur Schott, under Maj. Emory; and at Fort Yuma in 1855 by

* In this paper *Catostomus plebeius* (*Pantosteus plebeius*) and *Gila pulchella* (*Leuciscus nigrescens*) are credited to the "Rio Mimbres, tributary of the Rio Gila." But the Rio Mimbres is not a tributary of the Gila, but of Lake Guzman, in Chihuahua, and these two species are not known to occur in the Colorado Basin.

Maj. S. H. Thomas. This species was also collected in 1854 by Mr. Kruzfeld, under Lieut. E. G. Beckwith, but the exact locality is not known. Only three species are mentioned in this report as coming from the Colorado Basin, being the same described by Baird & Girard in 1853 *a*.

1859*a*. CHARLES GIRARD. Ichthyology of the Boundary. <Report of the United States and Mexican Boundary Survey, made under the direction of the Secretary of the Interior, by William H. Emory, Major, First Cavalry, and United States Commissioner. Vol. 3, Washington, 1858. Part on Ichthyology, 1859, 1–85, plates 1–40.

In this final report upon the fishes collected by this survey Girard mentions 17 species as having been obtained in the Colorado Basin. All of these were described in the Proceedings of the Academy of Natural Sciences for the years 1853, 1854, and 1856. Nothing new is added in the Mexican Boundary Report except plates containing illustrations of all the species.

Page.	Species as recorded.	Present identification.	Page.	Species as recorded.	Present identification.
37	Minomus insignis	Catostomus insignis.	61	Gila elegans	Gila elegans.
38	Minomus clarki.	Catostomus clarki.	61	Gila grahami	Gila robusta.
39	Acomus latipinnis........	Catostomus latipinnis.	62	Gila emorii	Gila elegans.
47	Argyreus osculus.........	Agosia oscula.	63	Tigoma intermedia	Leuciscus intermedia.
47	Argyreus notabilis	Agosia oscula.	64	Tigoma gibbosa...........	Leuciscus niger.
48	Agosia chrysogaster......	Agosia chrysogaster.	65	Ptychocheilus lucius	Ptychocheilus lucius.
49	Agosia metallica..........	Agosia chrysogaster.	68	Cyprinodon macularius...	Cyprinodon macularius.
50	Meda fulgida	Meda fulgida.	73	Girardinus occidentalis...	Heterandria occidentalis.
60	Tiaroga cobitis	Tiaroga cobitis.			

1859*b*. CHARLES GIRARD, M. D. Ichthyological Notices, XLI–LIX. <Proc. Ac. Nat. Sci. Phila. 1859, 113–122.

On page 119 of this paper Girard describes two female specimens of *Girardinus occidentalis* (= *Heterandria occidentalis*) obtained at Tucson, Ariz., by Arthur Schott, and numerous other specimens obtained at Tucson by Dr. A. L. Heermann.

1860. CHARLES C. ABBOTT. Descriptions of Four New Species of North American Cyprinidæ. <Proc. Ac. Nat. Sci. Phila. 1860, 473, 474.

This paper contains a description of *Gila affinis* (= *Gila robusta*), the specimens erroneously said to be from "Kansas."

1871. E. D. COPE, A. M. Recent Reptiles and Fishes. Report on the Reptiles and Fishes obtained by the Naturalists of the Expedition. <Hayden's Report Geol. Surv. Wyoming for 1870 (1871), 432–442.

In this report Prof. Cope records 13 species from the Colorado Basin, 5 of which he describes as new.

Page.	Species as recorded.	Present identification.	Page.	Species as recorded.	Present identification.
433	Uranidea punctulata....	Cottus bairdi punctulatus.	438	Hybopsis egregius	Leuciscus egregius
433	Salmo (Salar) virginalis.	Salmo mykiss pleuriticus.	441	Gila elegans	Gila elegans.
433	Coregonus williamsonii	Coregonus williamsoni.	441	Gila grahamii	Gila robusta.
434	Catostomus latipinne...	Catostomus latipinnis.	441	Gila gracilis..............	Gila robusta.
435	Catostomus *discobolus* ..	Catostomus latipinnis.	441	Gila *nacrea*	Gila robusta.
435	Minomus *delphinus*.....	Pantosteus delphinus.	442	Ceratichthys *squamilentus*.	Couesius squamilentus:
436	Minomus *bardus*........	Pantosteus delphinus.			

1872. EDWARD D. COPE, A. M. Report on the Recent Reptiles and Fishes of the Survey, collected by Campbell Carrington and C. M. Dawes. <Hayden's Report Geol. Surv. Montana for 1871 (1872), 467–476.

this report Prof. Cope records but one species from the Colorado Basin. This is *Salmo pleuriticus* (= *Salmo mykiss pleuriticus*), which he describes as new.

1874. EDWARD D. COPE, A. M. On the Plagopterinæ and the Ichthyology of Utah.

In this paper 10 species are credited to the Colorado Basin. Seven of these are described as new.

Page.	Species as recorded.	Present identification.	Page.	Species as recorded.	Present identification.
2	*Plagopterus argentissimus.*	Plagopterus argentissimus.	5	Rhinichthys henshavii, *Var. III.*	Rhinichthys cataractæ dulcis.
3	Meda fulgida	Meda fulgida.	6	Hybopsis *timpanogensis*	Leuciscus lineatus.
3	*Lepidomeda vittata*	Lepidomeda vittata.	8	Ceratichthys biguttatus	
4	Lepidomeda *jarrovii*	Lepidomeda jarrovii.	8	Ceratichthys *ventricosus*	Agosia oscula.
5	Rhinichthys henshavii, *Var. II.*	Rhinichthys cataractæ dulcis.	10	Catostomus discobolus	Catostomus latipinnis.

1876. Prof. E. D. COPE AND DR. H. C. YARROW. Report upon the Collections of Fishes made in portions of Nevada, Utah, California, Colorado, New Mexico, and Arizona, during the years 1871, 1872, 1873, and 1874. <Zoology of the Wheeler Survey west of the 100th meridian, 1875 (1876), 635–703, plates XXVI–XXXII.

This is by far the most important contribution to the literature of the ichthyology of the Colorado Basin that has yet appeared. The authors credit no fewer than 27 species to this basin.

In the body of the report 29 nominal species are recorded from Colorado Basin localities, but 4 of these were apparently erroneously so referred. They are *Gila montana* from "Arizona," *Gila pandora* from "Pagosa, Colo.," *Gila gula* from "Rio de Acama" and "near Fort Wingate, N. Mex.," and *Ptychostomus congestus* from "Ash Creek, Ariz." *Gila montana* (=*Leuciscus hydrophlox*) was probably from some place in the Utah Basin. Both *Gila pandora* and *Gila gula* are now regarded as being identical with *Leuciscus nigrescens*, a Rio Grande species, and Cope & Yarrow's specimens probably came from that basin. *Ptychostomus congestus* (*Moxostoma congestum*) is a Texan species, and the 3 specimens which Cope & Yarrow provisionally referred to this species may have come from some Texan locality.

In the recapitulation of species (p. 699) the authors name 27 species in the Colorado River list, 4 of which are not given in the body of the report, viz: *Ceratichthys squamilentus* (*Couesius squamilentus*), *Pantosteus bardus* (*Pantosteus delphinus*), *Pantosteus delphinus*, and *Coregonus williamsoni*. All of these are properly credited to the Colorado Basin, as had previously been determined by Prof. Cope.

Page.	Species as recorded.	Present identification.	Page.	Species as recorded.	Present identification.
640	Plagopterus argentissimus.	Plagopterus argentissimus.	665	Gila grahamii	Gila robusta.
642	Meda fulgida	Meda fulgida.	666	Gila nacrea	Gila robusta.
642	Lepidomeda vittata	Lepidomeda vittata.	666	Gila *seminuda*	Gila seminuda.
643	Lepidomeda jarrovii	Lepidomeda jarrovii.	667	Gila emorii	Gila elegans.
647	Apocope oscula	Agosia oscula	667	Siboma atraria	Leuciscus lineatus.
648	Apocope ventricosa	Agosia oscula.	668	Siboma atraria *longiceps*	Leuciscus lineatus.
648	Apocope *couesii*	Agosia couesii.	670	Hyborhynchus *siderius*	Agosia chrysogaster.
651	Ceratichthys biguttatus		674	Pantosteus jarrovii	Pantosteus delphinus.
663	Gila *nigra*	Leuciscus niger.	676	Catostomus insigne	Catostomus insignis.
663	Gila robusta	Gila robusta.	677	Catostomus discobolus	Pantosteus delphinus.
664	Gila elegans	Gila elegans.	693	Salmo pleuriticus	Salmo mykiss pleuriticus.
665	Gila gracilis	Gila robusta.	695	Girardinus sonoriensis	Heterandria occidentalis.
			696	Uranidea vheeleri	Cottus bairdi punctulatus.

1876. Prof. THEO. GILL. Report on Ichthyology. <Capt. Simpson's Report of Explorations across the Great Basin of the Territory of Utah, in 1859, 385–431.

In this report *Platygobio communis* (*Platygobio gracilis*) is credited to Green River, Utah, probably erroneously. *Potamocottus punctulatus* is described from a "single specimen obtained by Dr. George Suckley, in the summer of 1859, between Bridger's Pass and Fort Bridger."

1880. WM. N. LOCKINGTON. Description of a New Species of *Catostomus* (*Catostomus cypho*) from the Colorado River. <Proc. Ac. Nat. Sci. Phila. 1880, 237-240.

The single specimen upon which this species was based was obtained from the Colorado River at the mouth of the Gila by John E. Curry, esq., and presented to the Museum of the California Academy of Sciences.

1889. PHILIP H. KIRSCH. Notes on a Collection of Fishes obtained in the Gila River at Fort Thomas, Arizona, by Lieut. W. L. Carpenter, U. S. Army. <Proceedings of the United States National Museum, XI, 1888 (1889), 555-558.

This is a report upon a collection of 7 species of fishes sent by Lieut. Carpenter to the Museum of the University of Indiana. The author describes one new species (*Catostomus gila*) and one new genus (*Xyrauchen*).

Page.	Species as recorded.	Present identification.	Page.	Species as recorded.	Present identification.
555	Catostomus latipinnis	Catostomus latipinnis.	556	*Xyrauchen* cypho	Xyrauchen cypho.
555	Catostomus *gila*	Catostomus gila.	558	Ptychochilus lucius	Ptychocheilus lucius.
556	Catostomus insignis	Catostomus insignis.	558	Gila emorii	Gila elegans.
556	Catostomus clarki	Catostomus clarkii.			

1891. DAVID STARR JORDAN. Report of Explorations in Colorado and Utah during the summer of 1889, with an Account of the Fishes found in each River Basin examined. <Bull. U. S. Fish Commission, IX, 1889 (1891), 1-40, plates 1-5.

During these explorations Dr. Jordan was assisted by Prof. Barton W. Evermann, Mr. Bert Fesler, and Mr. Bradley M. Davis. Next to the Wheeler Survey the collections obtained by this party are the largest and most important that have yet come from the Colorado Basin. The collections contain 10 species and represent 18 Colorado Basin localities. The following is a list of the species contained in these collections:

Page.	Identification.	Page.	Identification.
26	Catostomus latipinnis..........................	27	Gila elegans.
26	Xyrauchen cypho..............................	28	Ptychocheilus lucius.
26	Xyrauchen *uncompahgre*	28	Agosia *yarrowi*.
27	Pantosteus delphinus	28	Salmo mykiss pleuriticus.
27	Gila robusta	29	Cottus bairdi punctulatus.

In August, 1893, while on their way to Idaho, the present writers stopped one day at Green River, Wyo., where the Green River was examined and a small collection of fishes made. The river was seined from a point about 1½ miles above the town down to below the railroad bridge. At that time (August 1) the stream averaged about 125 feet wide and at least 3 feet deep; the current flowed about 1½ feet per second, and the temperature was about 70° at noon. The water was very green where deep; though clear, it contains a good deal of alkali. The bottom of the channel is of gravel, shale, mud, and sand in different places. The shores are of adobe or sand and gravel where low, but of sandstone or shale where high. The left bank of the river above the town is of very high and picturesque cliffs and buttes of shale and sandstones of varied colors; and the deep side of the stream is at the foot of these cliffs. Seven species of fishes were obtained by us. These represent the result of almost constant seining for the greater part of a day, and thus indicate the paucity of species in this stream.

Our notes on this collection will be found under the appropriate species in the following list.

LIST OF SPECIES OF FISHES KNOWN FROM THE COLORADO BASIN.

In the following list we give under each species, in chronological order, the different places in the Colorado Basin from which it has been recorded. When a tabular form is used, the name under which the species was recorded is given in the first column, the locality from which recorded in the second, the name of the collector in the third, and the authority in the last. When two or more papers by the same author appeared in the same year, they are designated as *a*, *b*, *c*, etc. The names of species described as new from the Colorado Basin are printed in italics in connection with the type locality.

CATOSTOMIDÆ. (The Sucker Family.)

1. Pantosteus arizonæ Gilbert. Salt River, Tempe, Ariz. (type, Gilbert, 1895).

2. Pantosteus delphinus (Cope).

Nominal species.	Locality.	Collector.	Authority.
Minomus *delphinus*	Probably a tributary of Green River.	Hayden collection	Cope, 1871.
Minomus *bardus*	do	do	Do.
Pantosteus jarrovii	Zuñi River, New Mexico	H. W. Henshaw	Cope & Yarrow, 1876.
Do	Tierra Armarilla, New Mexico	Yarrow & Shedd	Do.
Pantosteus delphinus	Eagle River, Gypsum, Colo	Evermann & Davis	Jordan, 1889.
Do	Gunnison River, Delta, Colo	Jordan, Evermann, Fesler & Davis.	Do.
Do	Uncompahgre River, Delta, Colo	do	Do.
Do	Rio de las Animas Perdidas, Durango, Colo.	do	Do.
Do	Rio Florida, Durango, Colo	do	Do.
Do	Green River, Green River	Evermann & Rutter	Evermann & Rutter, 1895.

This species we found abundant in Green River. The specimens secured do not differ materially from those collected by Jordan & Evermann in the Gunnison and Uncompahgre rivers in 1889.

3. Pantosteus clarkii (Baird & Girard).

Nominal species	Locality.	Collector.	Authority.
Minomus *clarkii*	Rio Santa Cruz	John N. Clark	Baird & Girard, 1854.
Do	do	do	Girard, 1859.
Catostomus clarki	Gila River, Ft. Thomas, Ariz	Lieut. W. L. Carpenter	Kirsch, 1889.

4. Catostomus latipinnis (Baird & Girard).

Nominal species.	Locality.	Collector.	Authority.
Catostomus *latipinnis*	Rio San Pedro, tributary of Gila	John H. Clark	Baird & Girard, 1853*c*.
Acomus latipinnis	do	do	Girard, 1856 and 1859.
Catostomus latipinne	Green River	Hayden collections	Cope, 1871.
Catostomus latipinnis	do	Jordan, Evermann, Fesler & Davis.	Jordan, 1889.
Do	Gila River, Ft. Thomas, Ariz	Lieut. Carpenter	Kirsch, 1889.
Do	Gunnison River, Delta, Colo	Jordan, Evermann, Fesler & Davis.	Jordan, 1889.
Do	Uncompahgre River, Delta, Colo	do	Do.
Do	Green River, Green River, Wyo	Evermann & Rutter	Evermann & Rutter, 1895.

This was even more abundant at Green River than *P. delphinus* and was found in the same places as that species. They both seem to prefer rather deep, quiet pools with mud bottoms. These specimens agree with others from Delta, Colo., with which they have been compared. The species is close to *Catostomus griseus*, the latter having a longer, slenderer snout and smaller fins.

5. Catostomus gila Kirsch. Types taken in the Gila River at Fort Thomas, Ariz., by Lieut. W. L. Carpenter, and described by Kirsch in 1889.

6. **Catostomus insignis** Baird & Girard.

Nominal species.	Locality.	Collector.	Authority.
Catostomus *insignis*	Rio San Pedro	John H. Clark	Baird & Girard, 1854.
Do	do	do	Girard, 1856 and 1859.
Catostomus insigne	Ash Creek, Arizona	Dr. J. T. Rothrock	Cope & Yarrow, 1876.
Do	"New Mexico"	Dr. Oscar Loew	Do.
Catostomus insignis	Gila River, Ft. Thomas, Ariz	Lieut. Carpenter	Kirsch, 1889.

7. **Xyrauchen cypho** (Lockington).

Nominal species.	Locality.	Collector.	Authority.
Catostomus *cypho*	Colorado River at mouth of the Gila River.		W. N. Lockington, 1880.
Xyrauchen cypho	Gila River, Ft. Thomas, Ariz	Lieut. Carpenter	Kirsch, 1889.
Do	Green River, Blake City, Utah	Jordan	Jordan, 1889.
Do	Gunnison River, Delta, Colo	do	Do.
Do	Uncompahgre R., Delta, Colo	do	Do.

8. **Xyrauchen uncompahgre** Jordan & Evermann. Types taken in the Uncompahgre River near the railway station at Delta, Colo., by Jordan, Evermann, Fesler & Davis, and described by Jordan & Evermann in 1889.

CYPRINIDÆ. (The Minnow Family.)

The bulk of the species of the Colorado Basin belong to this family.*

9. **Ptychocheilus lucius** Girard.

Nominal species.	Locality.	Collector.	Authority.
Gila trout	Gila River	Lieut. Col. W. H. Emory	Emory, 1848.
Ptychocheilus *lucius*	Rio Colorado	A. Schott	Girard, 1856 and 1859.
Do	Gila River, Ft. Thomas, Ariz	Lieut. Carpenter	Kirsch, 1889.
Do	Gunnison River, Delta, Colo	Jordan, Evermann, Fesler & Davis.	Jordan, 1889.
Do	Uncomphagre R., Delta, Colo	do	Do.
Do	Green R., Blake City, Utah	do	Do.
Do	Green River, Green River, Wyo	Evermann & Rutter	Evermann & Rutter, 1895.

We did not secure any specimens of this large cyprinoid at Green River, but were told that it is a common fish in that part of the Green River. It is locally known as "whitefish," "white salmon," or "salmon," and individuals weighing 8 to 10 pounds are often taken with the hook.

10. **Gila elegans** Baird & Girard.

Nominal species.	Locality.	Collector.	Authority.
Gila *elegans*	Zuñi River	Dr. Woodhouse	Baird & Girard, 1853*a* and 1853*b*.
Gila *emoryi*	Near mouth of Gila River	John L. LeConte	Baird & Girard, 1853*c*.
Do	Gila River	do	Girard, 1856.
Gila elegans	Colorado River	A. Schott	Girard, 1856, 1858.
Gila emoryi	Gila River	John L. LeConte	Girard, 1858.
Gila elegans	Zuñi River	Dr. Woodhouse	Do.
Gila emoryi	Near mouth of Gila River	John L. LeConte	Girard, 1859.
Gila elegans	Colorado River, Cal	A. Schott	Do.
Do	Forks of Green River	Hayden collection	Cope, 1871.
Do	Ft. Bridger, Wyo	do	Do.
Do	San Juan River, New Mexico	Lieut. Birnie	Cope & Yarrow, 1876.
Do	Southwestern Arizona	F. Bischoff	Do.
Gila emorii	Gila River	Lieut. Carpenter	Kirsch, 1889.
Gila elegans	Gunnison River, Delta, Colo	Jordan, Evermann, Fesler & Davis.	Jordan, 1889.
Do	Green River, Blake City, Utah	Dr. Jordan	Do.

*Cyprinus carpio Linnæus. *The German Carp.* This species was introduced from Europe into the United States in 1875 by the Government, and even earlier by private individuals. From the ponds it has escaped to the rivers and is now found in many of the larger rivers, including the Colorado.

11. Gila robusta Baird & Girard.

Nominal species.	Locality.	Collector.	Authority.
Gila *robusta*	River Zuñi	Dr. Woodhouse	Baird & Girard, 1853*a*, 1853*b*.
Gila *gracilis*	do	do	Do.
Gila *grahami*	Rio San Pedro, tributary of Rio Gila	John H. Clark	Baird & Girard, 1853*c*.
Ptychocheilus *vorax*	Unknown	Lieut. Beckwith	Girard, 1856.
Gila robusta	River Zuñi	Dr. Woodhouse	Do.
Gila grahamii	Rio San Pedro, tributary of Rio Gila	John H. Clark	Do.
Gila gracilis	River Zuñi	Dr. Woodhouse	Girard, 1856, 1858.
Gila robusta	do	do	Girard, 1858, 1859.
Gila grahami	Rio San Pedro, tributary of Rio Gila	John H. Clark	Do.
Gila *affinis*	"Kansas"; evidently an error	W. A. Hammond	Abbott, 1860.
Leuciscus *zunnensis*	Zuñi River	Dr. Woodhouse	Günther, 1868.
Gila grahami	Ft. Bridger	Hayden collection	Cope, 1871.
Gila gracilis	do	do	Do.
Do	Henry's Fork of Green River	do	Do.
Gila grahamii	do	do	Do
Gila gracilis	Forks of Green River	do	Do.
Gila nacrea	do	Campbell Carrington	Do
Gila robusta	Gila River	H. W. Henshaw	Cope & Yarrow, 1876.
Gila grahamii	do	Jas. M. Rutter	Do.
Gila robusta	Arizona	H. W. Henshaw	Do.
Gila gracilis	White River, Arizona	do	Do.
Gila grahamii	do	Loew, Henshaw & Rutter	Do.
Do	Camp Apache	Dr. Loew	Do.
Do	Colorado Chiquito	Dr. Newberry	Do.
Do	Ash Creek, Arizona	Dr. Rothrock	Do.
Gila nacrea	Green River, Wyoming		Do.
Gila robusta	Uncompahgre R., Delta, Colo	Jordan, Evermann, Fesler & Davis.	Jordan, 1889.
Do	Gunnison River, Delta, Colo	do	Do.
Do	Green River, Green River, Wyo	Evermann & Rutter	Evermann & Rutter, 1895.
Do	Babacomari Creek, Ariz	Dr. A. K. Fisher	Do.

This species seems to be distributed throughout the Colorado River Basin and is extremely variable. Compared with specimens from Salt River at Tempe, Ariz., ours from Green River differ in the obviously smaller eye and the possibly wider union of the gill-membranes with the isthmus. If, on further investigation, a northern form is found separable from the southern, it will bear the name *nacrea* Cope. The following is a detailed description of the six examples taken by us in Green River at Green River, Wyo., near the type locality of *Gila nacrea*:

Head, $3\frac{3}{4}$ to 4; depth, $4\frac{3}{5}$ to $4\frac{9}{10}$; eye, $3\frac{3}{4}$ to 4; snout, $3\frac{1}{4}$ to 4; interorbital width, $2\frac{3}{4}$; D. 9 or 10; A. 9 or 10; scales, 23 to 25–85 to 103–13 or 14; teeth, 2, 5–4, 2, hooked, no grinding surface. Body moderately slender, head broad, the upper profile longitudinally and transversely convex; snout decurved; mouth oblique, jaws subequal, maxillary barely reaching beyond front of orbit, about as long as from tip of snout to pupil; interorbital space very convex, $1\frac{3}{5}$ times diameter of eye; back not strongly arched; caudal peduncle rather slender, compressed, the least depth 4 in head. Origin of dorsal behind insertion of ventrals, midway between nostrils and base of middle caudal rays; anterior dorsal rays somewhat produced, their length $1\frac{1}{7}$ in head; anal smaller, length of longest ray $1\frac{1}{3}$ in head, equal to length of pectoral; pectorals not quite reaching ventrals, the latter barely reaching vent, $1\frac{3}{5}$ in head; caudal widely forked, the lobes longer than head. Scales very small, crowded on back; lateral line strongly decurved.

Two of these specimens, $3\frac{1}{2}$ and 4 inches long, respectively, differ from the others in having a shorter, blunter head, and a slightly deeper caudal peduncle.

12. Gila seminuda Cope & Yarrow. Types taken in the Rio Virgen, Washington, Utah, and described by Cope & Yarrow in 1876.

13. Leuciscus lineatus (Girard).

Nominal species.	Locality.	Collector.	Authority.
Hybopsis *timpanogensis*	Gunnison River	Mr. Klett	Cope, 1874.
Do	do	do	Cope & Yarrow, 1876.
Siboma atraria	do	Mr. Henshaw	Do.
Do	Zuñi River	do	Do.
Do	Colorado Chiquito River, New Mexico.	do	Do.
Siboma atraria *longiceps*	Colorado Chiquito River	Dr. Newberry	Do.
Do	Snake Creek, Nevada	Dr. Yarrow	Do.
Do	Rio Virgen	do	Do.

14. Leuciscus intermedius (Girard). Types taken in the Rio San Pedro, tributary of Rio Gila, by John H. Clark, and described as *Tigoma intermedia* by Girard in 1856 and 1859.

15. Leuciscus niger (Cope).

Nominal species.	Locality.	Collector.	Authority.
Gila *gibbosa*	Rio Santa Cruz, tributary of Rio Gila.	John H. Clark	Baird & Girard, 1834.
Tigoma gibbosa	Tucson, Sonora, Ariz	Heermann & Clark	Girard, 1856, 1859.
Do	Rio Santa Cruz, tributary of Rio Gila.	John H. Clark	Girard, 1859.
Gila *nigra*	Ash Creek, Arizona	Dr. Rothrock	Cope & Yarrow, 1876.
Do	San Carlos, Arizona	H. W. Henshaw	Do.

16. Leuciscus egregius Cope. Types taken in the Green River by the Hayden expedition and described as *Hybopsis egregius* by Cope in 1871.

17. Tiaroga cobitis Girard. Types taken in the Rio San Pedro, tributary of Rio Gila, by John H. Clark, and described by Girard in 1856 and 1859.

18. Rhinichthys cataractæ dulcis (Girard).

Nominal species.	Locality.	Collector.	Authority.
Rhinichthys henshavii, *var. II*	Colorado Chiquito	H. W. Henshaw	Cope, 1874.
Rhinichthys henshavii, *var. III*	Camp Apache, Arizona	do	Do.

19. Agosia oscula (Girard).

Nominal species.	Locality.	Collector.	Authority.
Argyreus *osculus*	Babacomari, tributary of Rio San Pedro, tributary of Rio Gila.	John H. Clark	Girard, 1856, 1859.
Argyreus *notabilis*	Rio Santa Cruz	do	Do.
Ceratichthys *ventricosus*	From Arizona		Cope, 1874.
Apocope oscula	Camp Apache, Arizona	H. W. Henshaw	Cope & Yarrow, 1876.
Do	Zuñi River	G. M. Keasby	Do.
Do	Pagosa, Colorado	Yarrow & Allen	Do.
Apocope ventricosus	From Arizona		Do.
Do	From New Mexico		Do.

20. Agosia yarrowi Jordan & Evermann.

Nominal species.	Locality.	Collector.	Authority.
Agosia *yarrowi*	Tomichi Creek, Colo	Jordan, Evermann, Fesler & Davis.	Jordan, 1889.
Do	Gunnison River, Gunnison	do	Do.
Do	Gunnison River, Delta, Colo	do	Do.
Do	Uncompahgre River, Delta	do	Do.
Do	Green River, Blake City, Utah	Dr. Jordan	Do.
Do	Eagle River, Gypsum, Colo	Evermann & Davis	Do.
Do	Rio de las Animas Perdidas, Durango, Colo.	Jordan, Evermann, Fesler & Davis.	Do.
Do	Rio Florida, Durango, Colo	do	Do.
Do	Leiter Creek, Durango, Colo	do	Do.
Do	Green River, Green River, Wyo	Evermann & Rutter	Evermann & Rutter, 1895.

Our collection from Green River, Wyoming, contains 57 specimens, which we provisionally refer to this species. They show some differences, however, and may prove to be an undescribed species. The following is a description of these specimens: Head, 4; depth, $4\frac{1}{3}$; eye, 5; snout, $2\frac{2}{3}$; interorbital width, $3\frac{1}{3}$. D. I, 8; A. I, 7; scales, 13-73-10, about 30 before the dorsal. Body rather slender, compressed; head long, snout long; mouth inferior, horizontal; barbel present; opercle rather short and evenly rounded. Caudal peduncle long, compressed, and rather deep. Scales larger than in *A. yarrowi*, much reduced in size on back on anterior part of body; lateral line complete, nearly straight.

Fins moderate, the height of the dorsal 1⅓ in head, the free edge somewhat concave; origin of dorsal fin behind ventrals, midway between base of middle caudal rays and nostril; anal fin falcate, its anterior rays equal to longest dorsal rays; pectorals rather short, 1⅓ in head, not reaching ventrals; ventrals short, barely reaching front of anal fin; caudal fin widely forked. Color in alcohol, olivaceous above, with darker marbling and small dark spots scattered irregularly over back and sides, few of which are, however, found below lateral line; under parts pale straw-color or silvery; fins all plain. The numerous specimens show but little variation from the above description, except in the squamation; the number of scales in the lateral line varies from 70 to 76. Occasionally there are 9 dorsal rays; eye, 4½ to 5; depth, 4⅕ to 4⅓; head, 4 to 4¼. From specimens of *Agosia yarrowi*, from Gunnison, Colo., these differ in having larger scales (16–74 to 80–13 in *yarrowi*), deeper and more compressed caudal peduncle, and narrower head.

This species was found to be quite abundant at Green River. It seemed to go in schools and to be found in the current, where they were feeding upon the gravelly bottom. At some hauls of the seine none at all would be taken, while at others considerable numbers would be secured.

21. Agosia couesii (Yarrow). Types from near Camp Apache, Arizona, described as *Apocope couesi* by Yarrow in 1876, and recorded by Cope & Yarrow, 1876.

22. Agosia chrysogaster Girard.

Nominal species.	Locality.	Collector.	Authority.
Agosia *chrysogaster*	Rio Santa Cruz	John H. Clark	Girard, 1856, 1859.
Agosia *metallica*	Rio San Pedro, tributary of Rio Gila.	do	Do.
Hyborhynchus *siderius*	Camp Lowell, Arizona	Jas. M. Rutter	Cope & Yarrow, 1876.

23. Couesius squamilentus Cope. Types from Henry Fork of Green River, Hayden collection, described as *Ceratichthys squamilentus* by Cope, 1871.

24. Lepidomeda vittata Cope. Types collected in the Colorado Chiquito by Dr. Newberry, described by Cope in 1874, and again recorded by Cope & Yarrow, 1876.

25. Lepidomeda jarrovii Cope. Types collected in the Colorado Chiquito by Yarrow & Henshaw, and described by Cope in 1874, and recorded by Cope & Yarrow, 1876.

26. Meda fulgida Girard.

Nominal species.	Locality.	Collector.	Authority.
Meda *fulgida*	Rio San Pedro, tributary of Rio Gila.	John H. Clark	Girard, 1856, 1859.
Do	do	Yarrow & Henshaw	Cope, 1874.
Do	do	do	Cope & Yarrow, 1876.

27. Plagopterus argentissimus Cope. Types from San Luis Valley in western Colorado, described by Cope, 1874, and again reported by Cope & Yarrow, 1876.

28. Salmo mykiss pleuriticus (Cope).

Nominal species.	Locality.	Collector.	Authority.
Salmo (Salar) virginalis	Near Ft. Bridger, Wyo	Hayden collection	Cope, 1871.
Do	Henry Fork of Green River	do	Do.
Salmo *pleuriticus*	Headwaters of Green River	Carrington & Logan	Cope, 1872.
Do	White River, Ariz.	H. W. Henshaw	Cope & Yarrow, 1876.
	White Mountains, Ariz	do	Do.
	Pagosa, Colo	C. B. Aiken	Do.
Salmo mykiss pleuriticus	Trapper Lake, Colorado	Jordan, Evermann, Fesler & Davis.	Jordan, 1889.
Do	Eagle River, Gypsum, Colorado	Evermann & Davis	Do.
Do	Cañon Creek, Glenwood Springs, Colo.	Jordan, Evermann, Fesler & Davis.	Do.
Do	Sweetwater Lake, Eagle Co., Colo.	do	Do.
Do	Gunnison River, Gunnison, Colo	do	Do.
Do	Rio Florida, Durango, Colo	do	Do.

No trout were seen by us at Green River, but we were informed that they are occasionally taken there and that they are common further up the river in the small tributaries.

29. **Coregonus williamsoni** Girard. *Rocky Mountain Whitefish.* The only reference to this species which we have seen, applying to this basin, is that of Cope, 1871, who had specimens in the Hayden collections, probably from Green River, near Fort Bridger. Numerous young individuals were taken by us at Green River, Wyoming, where it is a common fish, attaining considerable size and being of value as a food-fish.

30. **Cyprinodon macularius** Baird & Girard. The types of this species were collected by John H. Clark in the Rio Gila and described by Baird & Girard in 1853 (*c*). In the Mexican Boundary Survey Girard credits the same specimens to the Rio San Pedro of the Gila. Only the types are known.

31. **Heterandria occidentalis** Baird & Girard.

Nominal species.	Locality.	Collector.	Authority.
Heterandria *occidentalis*	Rio Santa Cruz	John H. Clark	Baird & Girard, 1853 *c*.
Girardinus occidentalis	do	do	Girard, 1859 *a*.
Do	Tucson	Dr. Heermann; Arthur Schott	Girard, 1859 *b*.
Girardinus sonoriensis	Camp Lowell, Ariz	H. W. Henshaw	Cope & Yarrow, 1876.

32. **Cottus bairdi punctulatus** (Gill). *Blob; "Bullhead."*

Nominal species.	Locality.	Collector.	Authority.
Uranidea punctulata	Headwaters of Green River	Hayden collections	Cope, 1871.
Potamocottus punctulatus	Between Bridger Pass and Fort Bridger.		Gill, 1876.
Uranidea vheeleri	Rio San Juan, Pagosa, Colo	Yarrow & Aiken	Cope, 1876.
Cottus bairdi punctulatus	Eagle River, Gypsum, Colo	Evermann & Davis	Jordan, 1889.
Do	Roaring Fork, Glenwood Springs, Colo.	Jordan, Evermann, Fesler & Davis.	Do.
Do	Gunnison River, Gunnison, Colo.	do	Do.
Do	Gunnison River, Delta, Colo	do	Do.
Do	Rio Florida	do	Do.
Do	Leitner Creek, Durango, Colo	do	Do.
Do	Rio de las Animas Perdidas, Durango, Colo.	do	Do.
Do	Green River, Green River, Wyo	Evermann & Rutter	Evermann & Rutter, 1895.

The blob was quite abundant at Green River, but most of the individuals secured were young. They were found in greatest numbers in some small isolated ponds or pools on the river bank.

NUMBER 631 SEPTEMBER 24, 1963

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY
UNIVERSITY OF MICHIGAN
ANN ARBOR, MICHIGAN

SUMMARY OF LATE CENOZOIC FRESHWATER FISH RECORDS FOR NORTH AMERICA

BY TERUYA UYENO AND ROBERT RUSH MILLER

RECENT renewed interest in late Cenozoic fossil fishes has resulted, in large measure, from a combination of parallel circumstances: stimulation to his students and associates by Claude W. Hibbard, increasing availability of good osteological collections of modern species, and advances in knowledge of the comparative osteology of major groups of North American fishes. Results of paleoichthyological research—both published and in progress—indicate that the nomenclature and classification of numerous groups are badly outmoded. The present contribution is intended to help correct this situation, but the imperfect nature of fossil preservation and large gaps in the record render the task a formidable one.

Inadequate comparative material often led early workers to describe new taxa with little or no comprehension of their relationships to modern forms. Since little consideration was given to intraspecific and ontogenetic variation, several names were often applied to specimens that subsequent consideration strongly suggests pertain to a single species. Age determinations were not infrequently grossly in error. Thus, the Ree Hills beds of South Dakota, assumed for years to be Oligocene, are actually Pleistocene; the Tranquille beds of British Columbia, assigned to the Miocene, are now known to be Middle Eocene; and the abundant vertebrate remains from Fossil Lake and vicinity, Oregon, heretofore regarded to be Pleistocene only, probably include also Pliocene remains (see footnote 5, p. 24).

In this report we summarize what is known about the occurrence of Miocene to Pleistocene freshwater fishes in North America, evaluating the classification and dating wherever possible. This was accomplished by a thorough review of the literature, an examination of types and other museum material, by field work since 1960, and by maintaining a close liaison with paleontologists and geologists studying continental Cenozoic biotas, stratigraphy, and modern dating methods.

This review is divided into four parts: (1) a systematic list (Table 1) of the fishes regarded as valid species, arranged phylogenetically by family and alphabetically by genera and species, followed by the age and the authority; (2) an annotated list in which we comment on certain valid species and treat those described fossils that we feel are either unidentifiable, or synonyms, or are otherwise unavailable; (3) a description of the localities from which fossils have been described, arranged alphabetically by states of the United States followed by Canada and also according to assigned ages of the deposits, including the families of fishes taken; and (4) a list of the references consulted, which constitutes a review of the North American literature, including papers that contain some of the recent evidence for age determinations.

Certain forms, the status of which is too uncertain for confident allocation at this time, are included in the annotated list but do not appear in Table 1, although when described there usually was no indication of uncertainty. These are: a ray (?), *Oncobatis pentagonus* (Leidy, 1870); *Aphelichthys* (Cope, 1893) and *Oligobelus arciferus* (Cope, 1870), cyprinids of questionable generic status; ?*Sardinius blackburni* (Cope, 1891), assigned to the Myctophidae but determined herein as a cyprinid; *Leuciscus rosei* (Hussakof, 1916*a*), described as a cyprinid and treated under that family in the list, where it is shown to be a clupeiform; *Catostomites* and *Boreocentrarchus* (Schlaikjer, 1937), referred to the Catostomidae and Centrachidae, respectively, but of doubtful family allocation; and *Proballostomus* (Cope, 1891), originally placed in the Cyprinodontidae but reidentified by us as a cyprinid. Also, the fossil described as *Plancterus kansae*? (Stovall and McAnulty, 1939), a cyprinodontid, appears as *Menidia* sp. in Table 1, family Atherinidae, as reidentified by Hubbs (1942). The supposed occurrence of a loach (Cobitidae) in North America is also discussed in the annotated list.

The first reports to describe valid species based on North American Cenozoic freshwater fishes were published in 1870 by Cope and Leidy. Working independently, these men described fossils from Plio-Pleistocene beds of southwestern Idaho. Both workers, but especially Cope, dominated the contributions in this field before 1900. In the first half of the following century, Hay, Jordan, Eastman, Hussakof, Hubbs, Hibbard, Dunkle, Lucas, Miller, and other ichthyologists and vertebrate paleontologists sporadically reported their findings on fossil fishes from Cenozoic beds. There had been, however, no extensive work on any freshwater post-Oligocene fish fauna since Cope's time until 1954, when C. L. Smith published the first of a series of papers on the fishes unearthed with other vertebrates in the High Plains region by C. W. Hibbard and his parties from The University of Michigan. Since 1954, a number of papers have appeared on Miocene to Pleistocene fishes.

In this report, "Late Cenozoic" refers to the period between the beginning of the Miocene and the end of the Pleistocene, an approximate time span of 25,000,000 years (Kulp, 1961). This segment of Cenozoic time was selected largely because available studies demonstrate that pre-Miocene American fish faunas differ notably from later ones. For example, the relatively well-known Eocene ichthyofaunas from the Green River and Bridger formations bear little resemblance to the Recent freshwater fish fauna (Miller, 1959:192). Although only few fossil fishes are known from Oligocene beds, this period is considered to represent a transitional stage between Eocene and Miocene. The Florissant lake beds of Colorado (upper Oligocene) have yielded an archaic sucker of the genus *Amyzon* which also occurs in Eocene beds of British Columbia and in Miocene deposits of Nevada.[1] *Trichophanes,* an extinct genus of pirate perches, is associated with *Amyzon* in Nevada and Colorado. Miocene deposits have produced the earliest records of cyprinid and ictalurid fishes in North America, two families that comprise important elements of the Recent freshwater fauna. Though several genera and species became extinct around the end of the Pliocene, especially in western North America, the Pliocene freshwater fish faunas resemble the Recent ones. With few exceptions, Pleistocene fishes appear to be the same as their living relatives, except for distributional changes that reflect the climatic fluctuations of this period.

Fish fossils occur in different forms of preservation. Some of them appear as isolated bones scattered on the surface of the earth (the "float" of paleontologists); some are embedded in loose sandstone, various types of sedimentary rocks, or in hard concretions; and others are merely impressions of skeletons on sedimentary rocks, diatomaceous earth, or in thin shales.

In general, the age of fossil beds has been determined chiefly by the

[1] Webb, S. David, MS, "Fossil fish in the Great Basin," suggests that the age of the Nevada "Amyzon beds" is probably Oligocene.

associated fossil mammals, but more recently in some cases dating has been by Radiocarbon and Potassium-Argon methods. Consequently not all age assignments set forth herein have reached a level of precision that would satisfy the majority of workers. In this report, age determinations were verified in the "Index to the Geologic Names of North America," by Wilson, Keroher, and Hansen (1959), except for certain datings derived from recent research workers.

ACKNOWLEDGMENTS

In preparing this paper we have received much assistance from paleontologists, ichthyologists, and geologists. We are greatly indebted to our colleague, Claude W. Hibbard, who provided critical age data, encouraged the work, and read the manuscript. The following persons loaned types and other specimens or allowed us to examine material in their care: Bobb Schaeffer, American Museum of Natural History; C. Lewis Gazin and David H. Dunkle, U. S. National Museum; L. S. Russell and Don E. McAllister, National Museum of Canada; C. C. Lindsey, University of British Columbia; J. Arnold Shotwell, University of Oregon; and William L. Stokes, University of Utah. For assistance in field work we are grateful to William J. Breed, Leland Crummet, Carl L. and Clark Hubbs, John F. Lance, Neal McClymonds, Richard H. Olson, Charles A. Repenning, Dwight W. Taylor, and Ralph T. Winn. Gerald R. Smith, W. Daniel Sable, and Gifford H. Miller served as field assistants. We thank Reeve M. Bailey for aid in identification, and the following individuals for original information on dating of deposits: Jack F. Evernden, E. R. Hampton, Morris F. Skinner, and S. David Webb.

Completion of this contribution was made possible by grants from the National Science Foundation (G–15914, GB–735).

TABLE 1

RECORDS OF LATE CENOZOIC FRESHWATER FISHES IN NORTH AMERICA

Abbreviations: A—Aftonian interglacial; E—Early; I—Illinoian glacial; Int—Late Pliocene to early Pliestocene; L—Late; M—Middle; S—Sangamon interglacial; W—Wisconsin glacial; X—General occurrence; Y—Yarmouth interglacial. UMMP refers to The University of Michigan Museum of Paleontology. The taxa are arranged alphabetically within each family; those marked by an asterisk are extinct.

Taxon	Age: Mio.	Plio.	Int.	Pleis.	Locality and Source
Acipenseridae					
Acipenser					
?medirostris				W	Calif., Sinclair, 1904 (det. by D. S. Jordan)
sp.				L	Penn., Leidy, 1889
Lepisosteidae					
Lepisosteus					
osseus				X	S. Car., Hay, 1923
platostomus				X	Fla., Hay, 1917†
				LI	Kans., Smith, G. R., 1963
spatula				X	Fla., Hay, 1919 (as *Atractosteus lapidosus*)
	X?				N. Car., Hay, 1929 (as *Atractosteus emmonsi*)
		E			Okla., Smith, C. L., 1962
				S	Tex., Uyeno and Miller, 1962*a*
?spatula				X	Tex., Hay, 1926 (as *Atractosteus tristoechus?*)
sp.	X?				N. Car., Cope, 1869 (as *Pneumatosteus nahunticus*)
				A?	Fla., Hay, 1927 (det. by Gidley)
				I	Okla., Smith, C. L., 1954
				LI	Kans., Smith, C. L., 1958
				S	Tex., Dalquest, 1962
		E			Nebr., Smith, C. L., 1962
				S	Tex., Uyeno and Miller, 1962*a*
				S	Tex., Uyeno, 1963
Amiidae					
Amia					
calva				X	Fla., Hay, 1917 (as *Amiatus calvus*)
				X	Ill., Hay, 1923 (as *Amiatus calvus*)
		E			Nebr., Smith, C. L., 1962
Salmonidae					
Oncorhynchus					
sp.				X	Ore., Hubbs and Miller, 1948: 68
Salvelinus					
namaycush				Y?	Wisc., Hussakof, 1916*b* (as *Cristivomer namaycush*)

† As identified by Hay. Possibly this is *L. platyrhincus* De Kay, the common gar of the region today.

TABLE 1 (*Continued*)

RECORDS OF LATE CENOZOIC FRESHWATER FISHES IN NORTH AMERICA

Taxon	Age				Locality and Source
	Mio.	Plio.	Int.	Pleis.	
Salmo					
?salar Linnaeus				X	Quebec, Lambe, 1904
**copei*, n. sp.			X		Idaho, Cope, 1870 (as *Rhabdofario lacustris*); Uyeno and Miller (this report)
sp.			X		Idaho, Russell, 1902 (as *Rhabdofario* sp.)
Osmeridae					
?Osmerus					
sp.	M				Mont., Eastman, 1917
Esocidae					
Esox					
masquinongy				I	Okla., Smith, C. L., 1954
				LI	Kans., Smith, G. R., 1963
sp.				W	Tex., Uyeno, 1963
?Esox					
sp.		E			Okla., Smith, C. L., 1962
Cyprinidae					
Campostoma					
anomalum				I	Kans., Smith, G. R., 1963
?Campostoma					
sp.				S	Tex., Uyeno, 1963
**Diastichus*					
macrodon			X		Idaho, Cope, 1870, 1883
parvidens			X		Idaho, Cope, 1870; Uyeno, 1961
Dionda					
nubila				LI	Kans., Smith, G. R., 1963
Gila					
**altarcus*				X	Ore., Cope, 1878, 1883 (as *Anchybopsis altarcus*)
mohavensis				W	Calif., Buwalda, 1914, and Blackwelder and Ellsworth, 1936 (as *Siphateles mohavensis*)
cf. robusta		M			Ariz., Uyeno and Miller, 1964
sp.				W	Calif., Flint and Gale, 1958 (det., as *Siphateles*, by C. L. Hubbs)
?Gila					
**turneri*		E			Nev., Lucas, 1900 (as *Leuciscus turneri*); Miller, 1959
**?turneri*	M				Mont., Eastman, 1917
*n. sp.		M			Ariz., Uyeno and Miller, 1964
Hybognathus					
hankinsoni				LI	Kans., Smith, G. R., 1963
Hybopsis					
cf. *gracilis*				I	Okla., Smith, C. L., 1958

TABLE 1 (*Continued*)

RECORDS OF LATE CENOZOIC FRESHWATER FISHES IN NORTH AMERICA

Taxon	Age				Locality and Source
	Mio.	Plio.	Int.	Pleis.	
**Mylocyprinus*					
robustus			X		Idaho, Leidy, 1870; Cope, 1883; Uyeno, 1961
		M			Idaho, Uyeno, 1961
Mylopharodon					
conocephalus				W	Calif., Sinclair, 1904 (det. by Jordan)
**hagermanensis*			X		Idaho, Uyeno, 1961
				M	Idaho, Uyeno, 1961
?*Mylopharodon*					
**condonianus*			X		Idaho, Cope, 1883 (as *Leucus condonianus*)
*cf. *condonianus*			X		Idaho, Uyeno, 1961
		M			Idaho, Uyeno, 1961
Notemigonus					
crysoleucas				I	Okla., Smith, C. L., 1954
				W	Tex., Uyeno, 1963
Notropis					
**megalepis*		M			Kans., Smith, C. L., 1962
Pimephales					
promelas				I	Okla., Smith, C. L., 1958
				W	Saskatchewan, Uyeno and Miller, MS
Ptychocheilus					
?*grandis*				X	Calif., Sinclair, 1904 (det. by Jordan)
				X?	Calif., Jordan, 1927 (as *P. tularis*)
lucius				X	Ariz., Unreported material in UMMP
oregonensis			X		Idaho, Uyeno, 1961; this report
*n. sp		M			Ariz., Uyeno and Miller, 1964
Semotilus					
atromaculatus				LI	Kans., Smith, G. R., 1963
				LS	Kans., Hibbard, 1955:205 (det. by R. R. Miller; re-examined by us)
cf. *atromaculatus*				I	Okla., Smith, C. L., 1954, 1958
sp.				I	Okla., Smith, C. L., 1954
**Sigmopharyngodon*					
idahoensis			X		Idaho, Uyeno, 1961
*New genus					
n. sp.		M			Ariz., Uyeno and Miller, 1964
Catostomidae					
**Amyzon*					
mentalis	M				Nev., Cope, 1872; Webb, MS (Oligocene)
?*brevipinnis*	E?				Wash., Eastman, 1917
Carpiodes					
carpio				S	Tex., Dalquest, 1962
Catostomus					
commersoni				I	Okla., Smith, C. L., 1954

TABLE 1 (*Continued*)

RECORDS OF LATE CENOZOIC FRESHWATER FISHES IN NORTH AMERICA

Taxon	Age				Locality and Source
	Mio.	Plio.	Int.	Pleis.	
				I	Kans. and Okla., Smith, C. L., 1958
				LI	Kans., Smith, G. R., 1963
**cristatus*			X		Idaho, Cope, 1883
latipinnis				X	Ariz., Unreported material in UMMP
*"*reddingi*"			X		Idaho, Cope, 1883; Hussakof, 1908
**shoshonensis*			X		Idaho, Cope, 1883
Chasmistes					
**batrachops*				X	Ore., Cope, 1883 (as *Catostomus batrachops*)
sp.				X	Ore., Hubbs and Miller, 1948: 68
Ictiobus					
cf. *bubalus*		E			Okla., Smith, C. L., 1962
sp.				S	Tex., Uyeno and Miller, 1962; Dalquest, 1962
				LI	Kans., Smith, G. R., 1963
Moxostoma					
duquesnei				LI	Kans., Smith, G. R., 1963
Ictaluridae					
Ictalurus					
**benderensis*		L			Kans., Smith, C. L., 1962
**decorus*	X?	X?			Tex., Hay, 1924 (as *Ameiurus? decorus*)
	X				S. Dak., Smith, C. L., 1961
**lambda*		E			Kans., Hubbs and Hibbard, 1951; Smith, C. L., 1962
melas				I	Okla., Smith, C. L., 1954
				I	Kans. and Okla., Smith, C. L., 1958
				LI	Kans., Smith, G. R., 1963
nebulosus				L	Penn., Leidy, 1889 (as *Ameiurus atrarius*)
		M			Kans., Smith, C. L., 1962
punctatus				I	Okla., Smith, C. L., 1954
				LI	Kans., Smith, C. L., 1958
				S	Tex., Uyeno and Miller, 1962*a*
				LI	Kans., Smith, G. R., 1963
cf. *punctatus*		E			Nebr., Smith, C. L., 1962
**sawrockensis*		L			Kans., Smith, C. L., 1962
sp.				LS	Kans., Hibbard, 1955:205 (as *Ameiurus* sp.)
	X	X			Nebr., Matthew, 1918; Cook and Cook, 1933 (as *Ameiurus* sp.)
	X	X			Nebr., Matthew, 1924 (as *Ameiurus* sp.)
		E			Okla., Smith, C. L., 1962
				S	Tex., Uyeno and Miller, 1962*a*
				S & W	Tex., Uyeno, 1963
Pylodictis					
olivaris				S	Tex., Uyeno and Miller, 1962*a*

TABLE 1 (*Continued*)

RECORDS OF LATE CENOZOIC FRESHWATER FISHES IN NORTH AMERICA

Taxon	Age				Locality and Source
	Mio.	Plio.	Int.	Pleis.	
Cyprinodontidae					
Cyprinodon					
**breviradius*					Miller, 1945 ("Late Tertiary," Calif.)
Empetrichthys					
**erdisi*		M			Calif., Jordan, 1924*a* (as *Parafundulus erdisi*); Uyeno and Miller, 1962*b*
Fundulus					
**curryi*		X?			Calif., Miller, 1945
**davidae*			X?		Calif., Miller, 1945
**detillai*		M			Kans., Hibbard and Dunkle, 1942; Smith, C. L., 1962
diaphanus				X	S. Dak., Cope, 1891 (as *Gephyrura concentrica*)
**eulepis*		X?			Calif., Miller, 1945
**nevadensis*		E			Nev., Eastman, 1917 (as *Parafundulus nevadensis*)
**sternbergi*		M			Kans., Robertson, 1943
sp		X			Okla., Hubbs, 1942
				I	Okla., Smith, C. L., 1954 (as *Aplodinotus grunniens*)
				LI	Kans., Hibbard and Taylor, 1960 (as *Aplodinotus grunniens*)
		M			Calif., Uyeno and Miller, 1962*b*
		E			Okla., Smith, C. L., 1962 (as ?*Aplodinotus* sp.)
		L			Kans., Smith, C. L., 1962 (as ?*Aplodinotus* sp.)
?*Fundulus*	X				Calif., Pierce, 1959 (as unidentified cyprinodont); Uyeno and Miller, 1962*b*
Gasterosteidae					
Gasterosteus					
aculeatus				X	Ontario, Dawson, 1872
**doryssus*		E			Nev., Jordan, 1907 (as *Merriamella doryssus*); Webb, 1963
Pungitius					
**haynesi*		X?			Calif., David, 1945
Aphredoderidae					
**Trichophanes*					
hians	M				Nev., Cope, 1872; Webb, MS (Oligocene)
Centrarchidae					
Ambloplites					
cf. *rupestris*		L			Kans., Smith, C. L., 1962
Chaenobryttus					
**kansasensis*		M			Kans., Hibbard, 1936; Smith, C. L., 1962; see annotated list.

TABLE 1 (*Concluded*)

RECORDS OF LATE CENOZOIC FRESHWATER FISHES IN NORTH AMERICA

Taxon	Age				Locality and Source
	Mio.	Plio.	Int.	Pleis.	
Lepomis					
cyanellus				I	Okla., Smith, C. L., 1954
		L			Kans., Smith, C. L., 1962
				LI	Kans., Smith, G. R., 1963
?*humilis*				LI	Kans., Smith, G. R., 1963
				X	S. Dak., Cope, 1891 (as *Oligoplarchus squamipinnis*); this report
cf. *microlophus*		E			Nebr., Smith, C. L., 1962
sp.				X	Fla., Hay, 1923
				X	Ill., Hay, 1923
				S	Tex., Dalquest, 1962
				S & W	Tex., Uyeno, 1963
Micropterus					
salmoides				LI	Kans., Smith, G. R., 1963
cf. *Micropterus*					
sp.	X	X			Nebr., Matthew, 1924
		E			Kans., Smith, C. L., 1962
**Plioplarchus*					
septemspinosus	M				Ore., Cope, 1889*a*; Eastman, 1917: Pl. 22; Webb, 1963; see annotated list
Pomoxis					
**lanei*		M			Kans., Hibbard, 1936; see annotated list
Percidae					
Perca					
flavescens				X	S. Dak., Cope, 1891 (as *Mioplosus multidentatus*); see annotated list
				I	Kans. and Okla., Smith, C. L., 1954, 1958
cf. *flavescens*				LI	Kans., Smith, G. R., 1963
Sciaenidae					
Aplodinotus					
grunniens				W	Mich., Hubbs, 1940
				S	Tex., Dalquest, 1962; Uyeno and Miller, 1962*a*
Cottidae					
Cottus					
beldingi		E			Nev., Jordan, 1924*b*; Hubbs and Miller, 1948:26
?*Cottus*					
**divaricatus*			X		Ida. and Ore., Cope, 1883; see annotated list
Atherinidae					
Menidia					
sp.		X			Okla., Stovall and McAnulty, 1939 (as *Plancterus kansae?*); Hubbs, 1942

ANNOTATED LIST

Rajidae

Oncobatis pentagonus Leidy.—Age and locality in doubt (Leidy, 1870). This species, the type of which has not been found, is said to have come from the "Rocky Mountains." It was described at the same time as the extinct cyprinid, *Mylocyprinus robustus,* which is known thus far only from Plio-Pleistocene deposits in southern Idaho. Cope (1883:153) stated that Leidy did not characterize his genus *Oncobatis* and placed this species in the genus *Raja* (spelled *Raia*). He referred it to the "Idaho Lake" (Pliocene) formation in this statement: "A species said to have been found in the beds of this deposit." We do not believe that this fish, if a ray, was associated with *Mylocyprinus,* which commonly occurs with other minnows and with suckers and sunfishes—all true freshwater fishes. Furthermore, extensive collecting in the beds of the "Idaho Lake" in recent years has failed to yield a ray. The status of this fossil must therefore remain in doubt until the type specimen is found and the locality data are verified.

Lepisosteidae

Atractosteus.—This genus is considered to be a synonym of *Lepisosteus.*

Atractosteus emmonsi Hay.—Miocene?, North Carolina (Hay, 1929). The type specimen is a scale, described and figured by Emmons (1858) but without a specific name, which was supplied by Hay. We feel that the drawing of the type lacks characters to distinguish it from the alligator gar, *L. spatula* Lacépède.

Atractosteus lapidosus Hay.—Pleistocene, Florida (Hay, 1919). The types constitute an opercle and scales. Judging from the figures, this species is also a synonym of *L. spatula.*

Atractosteus tristoechus (Bloch and Schneider)?.—Pleistocene, Texas (Hay, 1926). Hay's queried identification was based on several scales which seem to represent *L. spatula.* Though the name *L. tristoechus* is now used for a species confined to Cuba, it was formerly used for the gar that is now called *L. spatula*—a species that occurs along the Gulf Coast and in the lower Mississippi River.

Pneumatosteus nahunticus Cope.—Miocene, North Carolina (Cope, 1869). This is probably a gar of the genus *Lepisosteus,* but the holotype, a caudal vertebra, is insufficient to assign it specifically.

Salmonidae

Oncorhynchus tshawytscha?.—Pleistocene?, Oregon (Jordan, 1907). There appear to be no objective data to support this identification which was based on numerous fragments of jaws, teeth, and vertebrae. The photographs of the specimens show that they bear close resemblance to "*Rhabdofario lacustris*" Cope from Idaho (=*Salmo copei*, see below).

Rhabdofario lacustris Cope.—Late Pliocene or early Pleistocene, Idaho (Cope, 1870). Examination of the type specimen and other material collected from the same formation (Cope's "Idaho Lake") in Idaho and Oregon shows that *Rhabdofario* should be synonymized with the genus *Salmo*. Since the combination *Salmo lacustris* dates from Linnaeus (1758:309), the fossil species described by Cope is herewith renamed *Salmo* **copei.** The diagnosis given by Cope will serve to distinguish it from its living relatives; the holotype is USNM 16352, the type of *R. lacustris*.

Cyprinidae

Alburnops angustarcus Cope.—Plio-Pleistocene?, Oregon (Cope, 1878). This was recognized as a valid species of the genus *Gila* by Uyeno (1961:340); however, we now consider it to be a synonym of *Gila altarcus* (Cope)—see the discussion under *Anchybopsis altarcus* Cope.

Alburnops gibbarcus Cope.—Plio-Pleistocene?, Oregon (Cope, 1878). This species, placed in the genus *Gila* by Uyeno (1961:341), is herein synonymized with *Anchybopsis altarcus* (=*Gila altarcus*; see below).

Alisodon mirus Hay.—Pleistocene, Texas (Hay, 1920). The type specimen is not a fish bone (Uyeno, 1961), and probably does not even represent the remains of an animal.

Anchybopsis altarcus Cope.—Plio-Pleistocene?, Oregon (Cope, 1878). This species was assigned to the genus *Gila* by Uyeno (1961:341). After careful study of numerous pharyngeals of *Gila* (*Siphateles*) *bicolor* (Girard), which most closely resembles this fossil, we conclude that the four species described by Cope (two in *Alburnops* and two in *Anchybopsis)* belong to a single taxon. As first revisers we select *Gila* (*Siphateles*) *altarcus* for this species because this name emphasizes a distinctive specific feature—namely, the elevated dentigerous surface of the pharyngeal arch. Thus, *G. angustarcus, G. gibbarcus,* and *G. breviarcus* are synonymized with *Gila altarcus.*

Anchybopsis breviarcus Cope.—Plio-Pleistocene?, Oregon (Cope, 1878). This nominal species, placed in *Gila* by Uyeno (1961:341), is discussed above.

Anchybopsis fasciolatus Cope.—Russell (1902), *nomen nudum* (see Hay, 1929).

Anchybopsis latus Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1870). The type (?) specimens, constituting very incomplete pharyngeal arches, bear some resemblance to those of *Diastichus parvidens* Cope. However, they lack the posterior edentulous process that characterizes the pharyngeal arch of that species. Consequently, we are uncertain as to the status of *A. latus,* although it may be the same as *D. parvidens.*

Aphelichthys lindahlii Cope.—Pleistocene?, Illinois (Cope, 1893). The type specimen has not been found and we are unable to identify the species from the original description.

Diastichus strangulatus Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1883). The type specimen, comprising only incomplete pharyngeals, is too fragmentary to enable us to determine its status (Uyeno, 1961:341).

Leucus condonianus Cope.—See ?*Mylopharodon condonianus* (Cope) in Table 1.

Leuciscus rosei Hussakof.—Middle Eocene, British Columbia (Hussakof, 1916*a*). The Tranquille beds that yielded this species were originally thought to be Miocene, which led to the belief that this record represents the earliest appearance of the Cyprinidae in North America (Miller, 1959:203). Recent dating of these beds by the Potassium-Argon method (Rouse and Mathews, 1961) gave an age of 49 million years, or Middle Eocene. An examination of the type specimens of *Leuciscus rosei* in the National Museum of Canada (Holotype, No. 2156, 2156*a*) and in the American Museum of Natural History (Paratype, No. 8059) shows conclusively that this species is not a cyprinid for the following reasons: there are two postterminal centra, as in the fossil clupeoid *Pterothrissus gissu* (Gosline, 1961: fig. 1A), and the three posterior vertebrae are upturned; there is no upright neural arch on the terminal vertebra; the hypurals are attached to the last three vertebrae (terminal and postterminal 1 and 2) rather than to the terminal vertebra; there are more than three branchiostegals (probably 7); there are many uniform-shaped, interneural spines; intermuscular bones are present; there is no trace of a Weberian apparatus; and there are teeth on the lower jaw and on the palatines (?) and pterygoids (?). Hay (1929:724) referred this species to the living American cyprinid genus *Richardsonius,* to which it bears a superficial appearance. *Leuciscus rosei* looks like a clupeiform fish, but we are not prepared to identify it further.

Leuciscus turneri Lucas.--See ?*Gila turneri* (Lucas) in Table 1.

Mylocyprinus inflexus Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1883). It seems that this species is not congeneric with *M. robustus* Leidy, but further study is necessary to determine its status (Uyeno, 1961:341).

Mylocyprinus kingii Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1870). This species is a synonym of *M. robustus* Leidy (Merrill, 1907:13; Uyeno, 1961:341).

Mylocyprinus longidens Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1870). This species is also a synonym of *M. robustus* Leidy (Uyeno, 1961:342).

Oligobelus arciferus Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1870). The holotype has evidently been misplaced and the status of this species is uncertain (Uyeno, 1961:342).

Oligobelus laminatus Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1870). This species, referred by Cope (1883:157) to the European genus *Squalius*, is a synonym of *Ptychocheilus oregonensis* (Richardson), as confirmed by new material collected by us in Idaho and compared with the holotype.

Proballostomus longulus Cope.—Pleistocene, South Dakota (Cope, 1891). This fish, assigned to the Cyprinodontidae by Cope, was treated in the same family by Rosen and Gordon (1953:38–9), who described and figured the anal-fin skeleton and associated vertebrae. However, we identify it as a cyprinid for the following reasons: the type specimen possesses a good tripus and a robust, modified rib of the 4th vertebra, both of which are parts of the Weberian apparatus; the hypural plate is made up of several (rather than two or less) hypural bones; and there are numerous intermuscular bones in the trunk and caudal regions. Dr. Rosen has re-examined the type and agrees with our conclusion. Since the associated fossil fishes from these beds are now all reidentified as living species (or very close relatives), we doubt that *Proballostomus* is a valid genus, but we are uncertain as to its status. Reasons for regarding the age as Pleistocene are given in the list of localities.

Ptychocheilus tularis Jordan.—?Pleistocene, California (Jordan, 1927). Judging from the description, locality, and probable age, this species seems to be a synonym of *P. grandis* (Ayres). The representatives of the genus *Ptychocheilus* in the Columbia River system (*P. oregonensis*) and in the Colorado River system (*P. lucius*) have undergone but little evolutionary change since Middle Pliocene time (Uyeno, 1961:334–35; Uyeno and Miller, 1964).

?*Sardinius blackburni* Cope.—Pleistocene, South Dakota (Cope, 1891). Although the holotype (AMNH 8091) lacks the head region, and we are not confident as to what genus it may pertain, we have no doubt that it represents a cyprinid fish. Consequently it cannot be referred to *Sardinius*, which is a member of the marine family Myctophidae.

Semotilus bairdii Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1870). The type specimen of this species has been misplaced or lost. Judging from the original description and our knowledge of the living and fossil material of *Ptychocheilus* from southern Idaho, we feel that *S. bairdii* is probably a synonym of *P. oregonensis* (Richardson).

Semotilus posticus Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1870). Study of variation in *Ptychocheilus oregonensis* (Richardson) and of new fossil material of this genus from Idaho convinces us that *S. posticus* is a synonym of *P. oregonensis*.

Siphateles.—This genus is regarded as a subgenus of Gila.[2]

Siphateles mohavensis Snyder.—See *Gila mohavensis* (Snyder) in Table 1.

Squalius reddingi Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1883). This species is a synonym of *Ptychocheilus oregonensis* (Richardson).

Catostomidae

Gerald R. Smith, currently studying the osteology of this family, provided the information given below under *Catostomus* and *Chasmistes*.

?*Catostomites alaskensis* Schlaikjer.—Early Oligocene to Early Miocene, Alaska (Schlaikjer, 1937). The types are so incomplete that even the family allocation is uncertain (R. R. Miller, *in* MacNeil *et al.*, 1961:1806).

Catostomus batrachops Cope.—See *Chasmites batrachops* (Cope) in Table 1.

Catostomus labiatus Ayres.—Pleistocene, Oregon (Cope, 1883; Starks, *in* Jordan, 1907). Misidentification. The specimens are not the Recent species *Catostomus occidentalis* (of which *C. labiatus* is a synonym—see Jordan, Evermann and Clark, 1930:738), but represent *Chasmistes batrachops* (Cope).

[2] Uyeno, Teruya, 1960. Osteology and phylogeny of the American cyprinid fishes allied to *Gila*. Ph.D. thesis, Univ. Mich., 174 pp. 35 pls.

Chasmistes spp.—Pleistocene, Oregon. Hubbs and Miller (1948:68, 74) and D. W. Taylor (1960:329) referred to sucker remains from Lower Klamath Lake and Fossil Lake as presumably *Chasmistes*; these references are too indefinite for allocation here.

Chasmistes oregonus Starks.—Pleistocene, Oregon (Starks, *in* Jordan, 1907). This species is provisionally synonymized with *Chasmistes batrachops* (Cope) on the grounds that the specimen referred by Starks to *Chasmistes* sp. appears to be intermediate between *C. oregonus* and *C. batrachops*. However, fossils collected at Fossil Lake represent more than one age (see list of localities) and there is a possibility that *oregonus* and *batrachops* are successional species. More extensive study of interspecific variation is required to clarify their status.

Cobitidae

In an attempt to evaluate the record by Cope (1873, 1883:161) of a loach of the genus *Cobitis* in western North America, in Plio-Pleistocene lake beds of southern Idaho, we sought in vain to locate the type material. Furthermore, extensive collecting in the same area, by us as well as by others, has failed to uncover remains that could possibly be referred to this wholly Old World family. We feel that Cope erred in his interpretation of the remains he briefly described (but did not figure), and hence we do not accept this record.

Ictaluridae

Ameiurus.—This genus is currently synonymized with *Ictalurus* (Taylor, W. R., 1954:43; Smith, C. L., 1961).

Ameiurus atrarius (De Kay).—Pleistocene, Pennsylvania (Leidy, 1889). This species is a synonym of *Ictalurus nebulosus* (LeSueur).

Ameiurus decorus Hay.—See *Ictalurus decorus* (Hay) in Table 1.

Ictalurus.—As indicated by Uyeno and Miller (1962*a*:340), the reference of pectoral spines from Plio-Pleistocene beds of southern Idaho and eastern Oregon to this genus (Cope, 1883:161, as ?*Amiurus* sp.; Miller, 1959:194, as *Ictalurus*) may have been premature. Hence these records are not included in Table 1.

Cyprinodontidae

Fundulus sternbergi Robertson—Middle Pliocene, Kansas. Although Miller (1955:12) wrote that this species is evidently the same as *F. detillai* Hibbard and Dunkle, from the same locality, and C. L. Smith (1962:512) synonymized the two species, we recognize both forms. The original descriptions contain a number of statements that clearly distinguish the two and we feel that study of the type specimens should be made before concluding that they are identical.

Gephyrura concentrica Cope.—Pleistocene, South Dakota (Cope, 1891). The holotype (AMNH 8089), a well-preserved specimen in fine condition, has been examined by R. M. Bailey as well as by us. There is no doubt that it is a species of *Fundulus*. Cope overlooked the well-developed conical teeth on the premaxillary; the bone is shaped much like that of *F. notti* (see Uyeno and Miller, 1962*b*: fig. 5D). Although incomplete posteriorly (only 9 rays remaining), the dorsal fin originated posterior to the insertion of the 7-rayed pelvics but anterior to the origin of the anal, which has 12 rays. The branchiostegals number 6, possibly 7. The total vertebral count (including the hypural plate) appears to be at least 32 to 34 (not 28, as recorded by Cope), but it is likely that more were present. There are about 18 principal caudal rays (33 total elements). The scales are of moderate size, perhaps 36 to 39 in the lateral series. The general shape of the body, position of fins, size of scales, and meristic data given above are in close agreement with those of *Fundulus diaphanus* (LeSueur), a species living today as far north as the Hudson Bay drainage of North Dakota (Miller, 1955:8). We, therefore, synonymize *Gephyrura concentrica* with *Fundulus diaphanus*.

Parafundulus.—This genus was synonymized with *Fundulus* by Miller (1945).

Parafundulus erdisi Jordan.—See *Empetrichthys erdisi* (Jordan) in Table 1.

Parafundulus nevadensis Eastman.—See *Fundulus nevadensis* (Eastman) in Table 1.

Plancterus kansae?.—This fossil is a species of *Menidia*, family Atherinidae; see Table 1.

Proballostomus longulus Cope.—See the family Cyprinidae in this list.

GASTEROSTEIDAE

Merriamella.—This genus is a synonym of *Gasterosteus* (Eastman, 1917:291).

Merriamella doryssa Jordan.—See *Gasterosteus doryssus* (Jordan) in Table 1.

Gasterosteus williamsoni leptosomus Hay.—Early Pliocene, Nevada (Hay, 1907). A synonym of *G. doryssus* (Jordan); see Jordan (1908).

CENTRARCHIDAE

Boreocentrarchus smithi Schlaikjer.—Early Oligocene to Early Miocene, Alaska (Schlaikjer, 1937). The type material of this species was examined many years ago by Reeve M. Bailey[3] who referred the species to the subfamily Centrarchinae, chiefly on the basis of the number of anal spines. Recent study of these specimens by Clarence L. Smith led him to feel (pers. comm.) that they are too incomplete (represented largely by impression) to identify confidently even to family level.

Chaenobryttus kansasensis Hibbard.—Middle Pliocene, Kansas (Hibbard, 1936). See below, under *Pomoxis lanei.*

?*Lepomis.*—The sunfish remains from Plio-Pleistocene deposits in southern Idaho and eastern Oregon, that were tentatively referred to the living genus *Lepomis* by Miller (1959:194), are receiving further study to clarify their status. Possibly a different Recent genus is involved. Hence this record is not given in Table 1.

Miocentrarchus Bailey, MS.—This name, used by Branson and Moore (1962:89), has not been formally proposed and hence is a *nomen nudum.*

Oligoplarchus squamipinnis Cope.—Pleistocene, South Dakota (Cope, 1891). Recent examination of the holotype (AMNH 8078) by R. M. Bailey and by us shows that this nominal species is a member of the genus *Lepomis,* to which Cope thought it was allied. The Pleistocene (rather than Oligocene) age of the beds containing the fossil, the known distribution of centrarchids in the region today (Bailey and Allum, 1962:95), and certain characters of the type (see Bailey, footnote 3) suggest that *O. squamipinnis* is close to, if not identical with, *Lepomis humilis* (Girard), present today in South Dakota.

Plioplarchus septemspinosus Cope.—Middle Miocene, Oregon (Cope, 1889*a*). Bailey (footnote 3) confirmed the tentative conclusion of Schlaikjer (1937) that this species is not referrable to *Plioplarchus,* and erected a new genus (*Miocentrarchus*) for its sole reception. Although still unpublished, Branson and Moore (1962:89) used the name.

Pomoxis lanei Hibbard.—Middle Pliocene, Kansas (Hibbard, 1936). Branson and Moore (1962:96) synonymized *Chaenobryttus kansasensis* with *C. gulosus* and *Pomoxis lanei* with *P. nigromaculatus,* stating that the fossil remains fall well within the limits of variation for these Recent species. We have not examined the holotypes of these two fossils. Bailey (footnote 3), however, stated that *Pomoxis lanei* is fully differentiated from the Recent species " . . . in the lower number of

[3] Bailey, Reeve M., 1938. A systematic revision of the centrarchid fishes, with a discussion of their distribution, variations, and probable interrelationships, Ph.D. thesis, Univ. Mich., 256 pp., 10 pls.

anal soft rays (12 instead of 17 to 20)." In discussing the phylogeny of sunfishes, Branson and Moore (1962:90) hypothesized that the lines containing *Pomoxis* and *Chaenobryttus*—the Centrarchinae and Lepominae, respectively—seemingly diverged during Plio-Pleistocene times. This conclusion contradicts their view (1962:96) that *Chaenobryttus gulosus* and *Pomoxis nigromaculatus* have not changed since Middle Pliocene (the age of the beds that yielded *C. kansasensis* and *P. lanei*). Under these circumstances, we tentatively recognize the two species described by Hibbard (see Table 1).

Percidae

Mioplosus multidentatus Cope.—Pleistocene, South Dakota (Cope, 1891). The holotype (AMNH 8075) of this nominal species has been examined by R. M. Bailey and by us, with the conclusion that it is identical with the living yellow perch, *Perca flavescens* (Mitchill). In agreement with the distinctive morphological characters of that species it has the following bones serrated (evidently the basis for the specific name): preopercular (the anterior serrations on the lower limb are strong and directed forward), cleithrum, and posttemporal, and probably the supracleithrum and subopercular. The two dorsal fins are separated; the spinous part has about 13 spines and the soft dorsal has the same number of rays. There is one interneural, 6 (probably 7) branchiostegals, and the frontal bone is roughened by ridges. Cope's low count of 31 vertebrae reflects the incompleteness of the type specimen, which lacks the caudal fin and much of the caudal peduncle. Jordan (1919) erected the genus *Eoperca* for the sole reception of this fossil, believing Cope's species to be intermediate between *Mioplosus* and *Perca*.

Sciaenidae

It now appears that the only valid fossil records of the freshwater drum (*Aplodinotus grunniens*) are for Michigan (Hubbs, 1940) and Texas (Dalquest, 1962; Uyeno and Miller, 1962*a*). The literature records cited below represent misidentifications for the cyprinodontid genus *Fundulus* (see Table 1); the materials were reidentified by Gerald R. Smith (see Hibbard, 1964).

Aplodinotus grunniens Rafinesque.—Pleistocene (Illinoian), Oklahoma (C. L. Smith, 1954). Equals *Fundulus* sp.

Aplodinotus grunniens Rafinesque.—Pleistocene (Illinoian), Kansas (Hibbard and Taylor, 1960:57). Equals *Fundulus* sp.

?*Aplodinotus* sp.—Pliocene (Early), Oklahoma; Late Pliocene, Kansas (C. L. Smith, 1962). Equals *Fundulus* sp.

Cottidae

We have examined the holotypes of the following species and believe three of these to be synonyms of "*Cottus*" *divaricatus*. The status of that species is briefly mentioned below.

Cottus cryptotremus Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1883). Synonym of *C. divaricatus* Cope.

Cottus divaricatus Cope.—See ?*Cottus divaricatus* Cope in Table 1. Although the type specimen and other referred materials are quite incomplete, it is almost certain that this species does not belong in the genus *Cottus*. The peculiar form of the preopercular spine and the apparently associated remarkable scale-like structures are unlike any known species of *Cottus*. However, since more material and further study are required to clarify the systematic status of this fish, we tentatively retain it in the genus *Cottus*.

Cottus hypoceras Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1883). Synonym of *C. divaricatus* Cope.

Cottus pontifex Cope.—Late Pliocene or Early Pleistocene, Idaho (Cope, 1883). Synonym of *C. divaricatus* Cope.

LOCALITIES YIELDING LATE CENOZOIC FRESHWATER FISHES IN NORTH AMERICA

Alaska

Oligocene (Early) to Miocene (Early)?.—About 80 mi. S of Fairbanks on N flank of Alaska Range (see Wahrhaftig, 1958), in Tertiary coal-bearing beds, about 6 1/2 mi. above mouth of Healy Cr. on E bank of small tributary entering from south; Schlaikjer, 1937: Catostomidae?, Centrarchidae?. Miller (*in* MacNeil *et al.*, 1961:1806) commented that the status of *Catostomites* is too indefinite for speculation. It and *Boreocentrarchus* (which may not be a sunfish) are discussed in the annotated list and are not listed in Table 1.

Arizona

Pleistocene.—Navajo Co., 2.7 mi. S of Taylor P. O., Snowflake fauna; material in UMMP (unreported): Cyprinidae, Catostomidae. For comments on age, based on mammals, see Lance (1960:157).

Pliocene (Middle).—Navajo Co., Bidahochi formation— (1) Roberts Mesa, 4.4 mi. by road NW of White Cone Trading Post; Uyeno and Miller, 1964: Cyprinidae. (2) Coliseum diatreme, near Indian Wells, about 35 mi. N of Holbrook (see Hack, 1942:354, pl. 1, no. 3); Uyeno and Miller, 1964: Cyprinidae. (3) White Cone, about 50 mi. N of Holbrook, White Cone fauna (Taylor, 1957), dated at 4.1 million years (Evernden *et al.*, 1963); Uyeno and Miller, 1964: Cyprinidae.

California

Pleistocene?.—Kings Co., in bed of Tulare Lake, near head of San Joaquin Valley, in white marl 12 ft. below lake bottom; Jordan, 1927: Cyprinidae.

Pleistocene (Wisconsin).—(1) San Bernardino Co., beds of Lake Manix, about 40 mi. E of Barstow; Blackwelder and Ellsworth, 1936; Hubbs *et al.*, 1962:227 (radiocarbon age 19,500 ± 500): Cyprinidae. (2) San Bernardino Co., Searles Lake (dry); Flint and Gale, 1958: Cyprinidae. (3) Shasta Co., Potter Cr. Cave, Sec. 25, T. 34 N, R. 4 W, Mt. Diablo Meridian; Sinclair, 1904: Acipenseridae, Cyprinidae.

Late Tertiary (Pliocene?).—Inyo Co., (1) 3 mi. SW of Chloride Cliffs in Funeral Mts., on E side of Death Valley National Monument; Miller, 1945: Cyprinodontidae. (2) About 6 mi. S of Furnace Cr. Ranch in Black Mts., on E side of Death Valley National Monument; Miller, 1945: Cyprinodontidae.

Age Unknown (Plio-Pleistocene?).—San Bernardino Co., near Black Mt. in Mohave Desert, about 40 mi. NW of Barstow and 25 mi. SE of Johannesburg; Miller, 1945: Cyprinodontidae.

Pliocene (Middle).—Los Angeles Co., (1) NW corner, Sec. 13, T. 6 N, R. 18 W, U.S.G.S. Tejon Quadrangle, part of Ridge Route formation; David, 1945: Gasterosteidae. (2) 1700 ft. W and 680 ft. S of NE corner, Sec. 25, T. 7 N, R. 19 W, Black Mt. Quadrangle, Piru Mts., Posey Canyon shale; Uyeno and Miller, 1962*b*: Cyprinodontidae. (3) 1000 ft. S and 1100 ft. E of NW corner, Sec. 2, T. 6 N, R. 18 W, Beartrap Canyon Quadrangle, Piru Mts., Posey Canyon shale; Uyeno and Miller, 1962*b*: Cyprinodontidae.

Miocene.—San Bernardino Co., Mule Cañon Drive, Calico Mts., Barstow formation (Palmer, 1957); Pierce, 1959: pl. 25 only (see Hubbs and Miller, 1962); Uyeno and Miller, 1962*b*: Cyprinodontidae.

Florida

Pleistocene.—(1) Levy Co., "Mixon bone bed," near Williston; Hay, 1919: Lepisosteidae. (2) St. Lucie Co., No. 3 or "Muck bed," Vero; Hay, 1917, 1919, 1923: Lepisosteidae, Amiidae.

Pleistocene (Aftonian?).—Brevard Co., Melbourne; Gidley *in* Hay (1927:274): Lepisosteidae.

Idaho

Pleistocene (Middle).—Owyhee Co., Jackass Butte, NE 1/4, Sec. 15, T. 4 S, R. 2 E; Uyeno, 1961, and unreported material at UMMP: Cyprinidae, Catostomidae (family only), Centrarchidae (family only).

Pliocene (Late) to Pleistocene (Early).—(1) Twin Falls Co., many localities in Glenns Ferry formation (Malde and Powers, 1962: 1206–09); Cope, 1870, 1883; Uyeno, 1961: Salmonidae, Cyprinidae, Catostomidae, Centrarchidae (genus undet., perhaps *Lepomis*), Cottidae. (2) Elmore Co., same as above. (3) Owyhee Co., same as above.

Pliocene (Middle).—Owyhee Co., NE 1/4, Sec. 12, T. 5 S, R. 1 W, Oreana Quadrangle, Chalk Hills formation (Malde and Powers, 1962); Uyeno, 1961: Cyprinidae.

Miocene (Late and Middle).—Nez Perce Co., 11 mi. E of Lewiston, T. 36 N, R. 4 W, Latah formation; Scheid, 1937: Cyprinidae (recorded as "*Leuciscus* skeletons"; not in Table 1).

Illinois

Pleistocene?: Pulaski Co.; Cope, 1893: Cyprinidae (see *Aphelichthys* in annotated list).

Pleistocene.—Around S end of Lake Michigan; Hay, 1923: Amiidae, Centrarchidae.

Kansas

Pleistocene (Late Sangamon).—Meade Co., XI Ranch in SW 1/4 Sec. 32, T. 33 S, R. 29 W, Jinglebob local fauna; Hibbard (1955:205): Cyprinidae, Ictaluridae.

Pleistocene (Late Illinoian).—Meade Co., (1) XI Ranch in SE 1/4 Sec. 32, T. 34 S, R. 29 W, Butler Spr. local fauna locality; Smith, C. L., 1958: Lepisosteidae, Catostomidae, Ictaluridae, Percidae. (2) Two localities, SW 1/4 Sec. 13 and SE 1/4 Sec. 14, T. 32 S, R. 29 W, and one locality in SE 1/4 Sec. 18, T. 32 S, R. 28 W; Smith, G. R., 1963: Lepisosteidae, Esocidae, Cyprinidae, Catostomidae, Ictaluridae, Percidae, Centrarchidae.

Pliocene (Late).—(1) Seward Co., Sawrock Canyon, Sec. 36, T. 34 S, R. 31 W, Rexroad formation; Smith, C. L., 1962: Ictaluridae, Cyprinodontidae. (2) Meade Co., four localities in Rexroad formation; Smith, *op. cit.*: Cyprinidae (family only), Ictaluridae, Centrarchidae, Cyprinodontidae.

PLIOCENE (MIDDLE).—Logan Co., Sec. 7, T. 11 S, R. 37 W, Ogallala formation; Hibbard and Dunkle, 1942; Robertson, 1943; Smith, C. L., 1962: Cyprinidae, Ictaluridae, Cyprinodontidae, Centrarchidae.

PLIOCENE (EARLY).—Trego Co., Sec. 15, T. 11 S, R. 22 W, Ogallala formation; Hubbs and Hibbard, 1951: Ictaluridae.

MONTANA

MIOCENE (MIDDLE).—Gallatin Co., Madison Valley, 4 mi. S of Three Forks; Eastman, 1917; Webb, MS: Osmeridae, Cyprinidae.

NEBRASKA

PLIOCENE (EARLY).—Brown Co., Sec. 33, T. 33 N, R. 23 W, Lower Valentine formation; Smith, C. L., 1962: Lepisosteidae, Amiidae, Ictaluridae, Centrarchidae.

MIOCENE (LATE) TO PLIOCENE (EARLY).—Sioux Co., Snake Cr. and Sheep Cr., about 20 mi. S of Agate; Cook and Cook, 1933:44; Matthew, 1918, 1924: Ictaluridae, Centrarchidae.

NEVADA

PLIOCENE (EARLY).—Churchill Co., (1) cave on E side of Carson Sink, about 5 mi. S of Stillwater, Truckee formation?; Jordan, 1924*b*; Webb, MS: Cottidae. (2) 3 mi. SW of Hazen, SW 1/4, Sec. 8, T. 19 N, R. 26 E, Truckee formation (Early Pliocene, rather than Pleistocene, dating for formation was recorded by Miller, 1955:12); Hay, 1907; Jordan, 1907; Eastman, 1917: Cyprinodontidae, Gasterosteidae.

MIOCENE TO PLIOCENE.— (1) Esmeralda Co., NE end of Silver Peak Range in extreme SW end of Big Smokey Valley; Lucas, 1900; Hubbs and Miller (1948:46): Cyprinidae, Catostomidae (family only). (2) Mineral Co., Stewart Valley, 25 mi. E of Mina; Webb, MS: Salmonidae, Cyprinidae (family only, as det. by us).

MIOCENE?.—Elko Co., 15.5 mi. by dirt road SE and W of Winecup Ranch (old Wilkins Ranch), about 25 mi. NE of Wells, Humboldt formation; material examined at Univ. of Utah: Centrarchidae (family only).

MIOCENE (LATE TO MIDDLE).—Washoe Co., Virgin Valley, N part of T. 45 N, R. 31 E, in extreme NW Nevada (Webb, MS); Hubbs and Miller (1948:26): Cyprinidae (family only).

MIOCENE (MIDDLE).[4]—Elko Co., 25 mi. NE of Elko, near Osino, lower part of Humboldt formation; Cope, 1872: Catostomidae, Aphredoderidae.

NORTH CAROLINA

MIOCENE?.—(1) Wayne Co., Nathan Edgerton Plantation; Cope, 1869: Lepisosteidae. (2) Brunswick Co., Cape Fear; Emmons, 1858; Hay, 1929: Lepisosteidae.

OKLAHOMA

PLEISTOCENE (ILLINOIAN?).—(1) Beaver Co., SE corner of Sec. 6, T. 5 N, R. 28 ECM, near Gate Ash Pit, 4 1/2 mi. N and nearly 1 mi. W of Gate; Smith, C. L., 1954: Lepisosteidae, Esocidae, Cyprinidae, Catostomidae, Ictaluridae, Cyprinodontidae, Centrarchidae, Percidae. (2) Harper Co., N 1/2 of SW 1/4, Sec. 10, T. 27 N, R. 24 W, Doby Spring locality; Smith, C. L., 1958; Stephens, 1960: Cyprinidae, Catostomidae, Ictaluridae, Centrarchidae, Percidae.

PLIOCENE.—Roger Mills Co., NE 1/4 of NE 1/4, Sec. 8, T. 2 N, R. 23 W, 5 mi. S and 1 1/2 mi. E of Cheyenne; Stovall and McAnulty, 1939; Hubbs, 1942: Cyprinodontidae.

PLIOCENE (EARLY).—Beaver Co., NE 1/4, Sec. 4, T. 3 N, R. 28 ECM and two other localities of Laverne formation; Smith, C. L., 1962: Lepisosteidae, Catostomidae, Ictaluridae, Cyprinodontidae, Centrarchidae (family only).

OREGON

PLEISTOCENE[5].—(1) Klamath Co., Lower Klamath Lake; Cressman, 1942: Salmonidae, Catostomidae (see Hubbs and Miller, 1948:68). (2) Klamath Co., Lost R., diatomaceous deposit; Jordan, 1907: Salmonidae (family only). (3) Lake Co. (a) Silver Lake, Cope, 1883; Catostomidae; (b) near Fossil Lake, Starks *in* Jordan, 1907: Catostomidae; and (c) Fossil Lake, Cope, 1883, 1889*b*; Jordan, 1907; Allison, 1940; Hubbs and Miller, 1948: Salmonidae, Cyprinidae, Catostomidae.

PLIOCENE (LATE) TO PLEISTOCENE (EARLY).—Baker Co., Willow Creek; Cope, 1883: Cottidae (see annotated list); unreported material examined at Yale University: Cyprinidae, Catostomidae.

[4] See footnote 1.

[5] The three localities in Lake Co. very probably include fossils of Pliocene as well as of Pleistocene age (E. R. Hampton, pers. comm.).

Pliocene (Middle).—Jefferson Co., Gravel pit. about 1 mi. by road WSW of Gateway; examined by us (age det. by A. J. Shotwell, pers. comm.): Salmonidae (family only).

Miocene (Middle).—Grant Co., Sec. 14, T. 13 S, R. 28 E, NE rectangle of Alrich Mt. quadrangle, 13 mi. E of Dayville and 0.1 mi. W of milepost 144 on John Day Highway (see Webb, MS); Cope, 1889*a*: Centrarchidae.

Pennsylvania

Pleistocene (Late).—Bucks Co., Durham Cave, near Riegelsville; Leidy, 1889: Acipenseridae, Ictaluridae.

South Carolina

Pleistocene.—Charleston Co., (1) Ashley R., bed elevated only a few ft. above tide-level of South Carolina coast; Hay, 1923: Lepisosteidae. (2) Young Id., Wadmalaw Sound, nearly 20 mi. SW of Charleston; Hay, 1923: Lepisosteidae.

South Dakota

Pleistocene.—Hand Co., Ree Heights or Ree Hills, on Leonard Fawcett Farm, NE 1/4, Sec. 21, T. 111 N, R. 70 W; Cope, 1891: Cyprinidae (see *Proballostomus* and *Sardinius* in annotated list), Cyprinodontidae, Centrarchidae, Percidae. In describing fossils from this locality, Cope thought they might be of Oligocene age; Wilson *et al.* (1959:541) listed the deposit (under Ree beds) as Eocene or Oligocene. At Bobb Schaeffer's request, Morris F. Skinner studied the geology and stratigraphy of the beds, concluding (pers. comm.) that they are Pleistocene. This is in accord with our findings that the identifiable fossil fishes from these beds are all Recent species.

Miocene (Early).—Bennett Co., Jim Ross Ranch, W of Martin, Flint Hill fauna; Smith, C. L., 1961: Ictaluridae.

Texas

Pleistocene.—San Patricio Co., about 20 mi. SW of Refugio and 1 mi. N of railroad bridge crossing Aransas R.; Hay, 1926: Lepisosteidae.

Pleistocene (Wisconsin).—Delta Co., five quarry sites near state higway 38 bridge across Sulphur R., just N of Ben Franklin, Sulphur R. formation; Uyeno, 1963: Esocidae, Cyprinidae, Catostomidae (family only), Ictaluridae, Centrarchidae.

Pleistocene (Sangamon).— (1) Denton Co., Trietsch Pit in second terrace above Clear Cr., on NE side of cr. and 7 mi. upstream from its junction with Elm Fork of Trinity R.; Uyeno, 1963: Lepisosteidae, Cyprinidae, Catostomidae (family only), Ictaluridae, Centrarchidae. (2) Dallas Co., T-2 terrace of Trinity R. on S side of Dallas; Uyeno and Miller, 1962*a*: Lepisosteidae, Catostomidae, Ictaluridae, Sciaenidae. (3) Foard Co., almost at E base of Texas Panhandle, Good Cr. formation; Dalquest, 1962: Lepisosteidae, Cyprinidae (family only), Catostomidae, Ictaluridae, Centrarchidae, Sciaenidae.

Miocene (Late) or Pliocene (Early).—Grimes Co., Jesse Garvin Farm, about 2 1/4 mi. due N of Navasota; Hay, 1924: Ictaluridae.

Utah

Pliocene (Middle).—Cache Co., Cache Valley, Salt Lake formation (Brown, 1949); material examined by us in USNM and UMMP: Cyprinidae (family only).

Washington

Miocene (Early?).—Ferry Co., near Republic; Eastman, 1917: Catostomidae.

Wisconsin

Pleistocene (Yarmouth?).—Dunn Co., clay beds at Menomonie in valley of Red Cedar R.; Hussakof, 1916*b*: Salmonidae.

Canada

Pleistocene.— (1) Ontario, Ottawa Valley, near Ottawa; Dawson, 1872: Gasterosteidae. (2) Quebec, Goose R., N shore of St. Lawrence R.; Lambe, 1904: Salmonidae.

Pleistocene (Wisconsin).—Saskatchewan, Lillestrom, 16 mi. SW of Moose Jaw (W of Regina) and just N of Johnstone Lake (age about 10,000 years); Uyeno and Miller, MS: Cyprinidae.

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Accepted for publication May 28, 1963

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[ca 1960's]

QUATERNARY FRESHWATER FISHES OF NORTH AMERICA*

ROBERT RUSH MILLER[1]

EXCEPT FOR a few ancient relicts—the sturgeons (*Acipenser*, *Scaphirhynchus*), paddlefish (*Polyodon*), gars (*Lepisosteus*), and bowfin (*Amia*), which have survived in and spread from old lowlands represented today by the Mississippi Valley—the origin of the freshwater fish fauna of North America barely antedates the Cenozoic Era. The most abundant family, the minnows (Cyprinidae), with approximately 250 species, appears no earlier in North America than the Miocene (Table 1). A diverse assemblage of species of widely different ages comprises this fauna, which may be divided into the true freshwater fishes and those that inhabit fresh water but tolerate salinities of various degrees. This division is in part arbitrary because some species and genera in the second group appear to be as restricted to fresh water as those in the first, but the distinction is important in understanding distributional patterns. Fishes long and sharply restricted to fresh water are able to disperse widely only with the relatively slow physiographic changes of the land itself.

The strictly freshwater (stenohaline) or Primary[2] fishes of North America (from the Rio Usumacinta basin of Guatemala-Mexico northward) comprise 15 families, about 90 genera, and approximately 500 species. (These figures are original estimates and include undescribed as well as described species.) The immediate precursors of 49 of these genera and 317 of the species, or about 60% of the living fauna, may well be no older than late Miocene or early Pliocene. The Secondary, Diadromous, Vicarious, Sporadic, and Complementary freshwater fishes include those that are salt-tolerant, regularly migrate between fresh water and the sea, are essentially freshwater representatives of chiefly marine groups, occur sporadically in fresh water, or invade fresh water chiefly where Primary fishes are reduced or absent. Some arbitrary decisions on the inclusion or exclusion of species were made. These fishes are treated here because some of them enter the fossil record. The North American fishes in this second group of categories comprise 25 families, about 100 genera, and approximately 400 species. (This includes, for Guatemala and Mexico, only those families recorded from fresh water north of the boundary between Mexico and United States.) When added to those in the first group, the total for all categories in North America (as restricted above) is about 940 species.

Considering only Primary freshwater fishes, the North American fauna includes seven endemic families: Amiidae (bowfin), Hiodontidae (mooneyes), Ictaluridae (North American catfishes), Amblyopsidae (cavefishes), Percopsidae (trout-perches), Aphredoderidae (pirate perches), and Centrarchidae (sunfishes). All except the Amblyopsidae are known from Cenozoic deposits and all except *Amia* are Recent or fossil only in North America; *Amia* is reported also from the Paleocene of Europe. Seven Primary families are shared with Eurasia: Polyodontidae (paddlefishes), Esocidae (pikes), Umbridae (mudminnows), Dalliidae (blackfishes), Cyprinidae (minnows), Catostomidae (suckers), and Percidae (perches). No fossils of the Umbridae are known in North America (but there are early Cenozoic records for Europe), and no known fossil record exists in either continent for the Arctic Dalliidae. The remaining five families have living representatives in both areas, and all but the Polyodontidae have a fossil record in Eurasia and North America; fossil paddlefishes are known from North America only (Cretaceous and Eocene, see MacAlpin, 1947). Only one freshwater family, the Characidae (characins), is common to North and South America, and the single species that occurs in the United States, *Astyanax fasciatus* (Cuvier), is able to tolerate brackish water (I found it living with euryhaline fishes around mangroves in Campeche, Mexico, in 1959).

Five secondary families that have known representatives in sea water or that may include salt-tolerant species (Goodeidae) are considered here especially for their zoogeographic interest. The Lepisosteidae (gars) and Goodeidae (Mexican livebearers) are North American endemics, the gars occurring as far southward as Costa Rica. The principally tropical Poeciliidae (livebearers) occur both in North and South America (Rosen and Bailey, 1963, p. 35, map 1), but have radiated from Middle America and probably originated there (Miller, 1959, p. 195; Rosen and Bailey, 1963, p. 144). The Cyprinodontidae (killifishes), chiefly of tropical and warm-temperate distribution (Lagler *et al.*, 1962, map, p. 465), occur on all continents save Australia; their comparative osteology has been treated by Sethi (1960), with some recent amplification by Uyeno and Miller

* I am grateful to the following for assistance in the preparation of this paper: J. R. Alcorn, Shelton P. Applegate, Reeve M. Bailey, Robert C. Bright, Ted M. Cavender, William L. Cristanelli, W. I. Follett, Maurice J. Grolier, Eugene R. Hampton, Claude W. Hibbard, F. D. Holland, Jr., David M. Hopkins, P. F. Karrow, C. C. Lindsey, Richard H. Olson, R. B. Peters, Donald E. Savage, Gerald R. Smith, R. H. Tedford, Teruya Uyeno, and Eugene Van Buren. Financial assistance was generously provided through grants from the National Science Foundation (G-15914, GB-735).

[1] Museum of Zoology, University of Michigan, Ann Arbor, Michigan.

[2] Myers (1951, p. 12) has defined this and the following terms.

late-Cenozoic fishes, it is the students of the living forms that are currently doing most of the research on Pleistocene and late-Tertiary fish faunas.

Although the time is far from ripe for a comprehensive synthesis of American paleoichthyology, considerable progress has been made in recent years toward broadening the scope of investigations so that they now focus on and contribute to related disciplines in both the biological and geological sciences. Hopefully we may expect to find some "index fossils" among the fishes that will provide evidence on the age and correlation of beds, although more secure evidence is likely to come from the composition of faunas. The horizons are unlimited, and I eagerly anticipate that much of what is presented here will rapidly become obsolete—particularly the information in Table 1, which marks the first attempt at such a tabular summary for fishes.

Only very recently have the published records of late Cenozoic continental fishes been summarized for North America, along with an evaluation of their classification and dating (Uyeno and Miller, 1963). The present chapter represents, in part, an updating and expansion of that paper. No fishes have yet been described from Pleistocene freshwater deposits in Mexico, but a fossil catfish from the bottom of Lago de Chapalá, close to and possibly identical with the living species *Ictalurus dugesii*, is under study by W. I. Follett of the California Academy of Sciences; fish remains have also been recorded from the adjacent Chapala formation (Downs, 1958; Clements, 1963). The fossils discussed herein are all from deposits in the continental United States and Canada (Fig. 1).

Fifteen families of American freshwater fishes are represented by 49 genera that are either living today (45) or became extinct near the onset of the Pleistocene. These 49 genera comprise 95 species, of which 5 belong to the 4 extinct genera (Table 1). Seven of the families, 34 of the genera, and 65 of the species are Primary fishes. The extinct genera, all from Plio-Pleistocene lake beds (the "Idaho Lake") in southern Idaho, are treated in the section on Paleohydrology. The three families of pre-Tertiary origin that include the sturgeons, gars, and bowfin are indicated (for my purposes here) as ubiquitous in the fossil record, although the known data show gaps for the late Cenozoic (Uyeno and Miller, 1963, p. 5). The 45 living genera comprise some 90 species, an increase of 6 genera and 19 species over the comparable data given by Uyeno and Miller (1963). Unlike that summary, however, the present one includes much unpublished information. In contrast to the 90 species of these 45 living genera that are now known as fossil, the same genera are represented by 418 living species —a strong indication of the incompleteness of the fossil record. Nearly half (41) of the known fossil species are extinct. Considering only the Pleistocene representatives of living genera, there are 14 families (eliminating the Atherinidae, not known fossil later than the Pliocene), 41 genera, and 69 species. These fishes are treated in the following section.

PLEISTOCENE FISHES

The known fossil record of North American late-Pliocene and Pleistocene freshwater fishes is indicated in Table 1 and by the sites shown in Figure 1. Only at relatively few of these localities—sites 11, 14-17, 25-32, and 34—are the recovered fossils sufficiently diversified to be regarded as comprising a fauna. Most if not all of the Pleistocene fishes recovered thus far, especially post-Nebraskan remains, are osteologically indistinguishable from living species; the few exceptions pertain chiefly to the "Idaho Lake" fauna, which includes some minnows, suckers, a catfish, and a sunfish that range in age from late Pliocene to early Pleistocene (Miller and Smith, MS). A few middle- to late-Pliocene species, other than ancient types, have been identified with existing forms (Uyeno and Miller, 1963, Table 1). Since the fossil records of sturgeons, gars, and bowfin contribute no new information concerning their distribution, evolution, or paleoecology, these relict forms are not considered further here.

Salmonidae. The trouts and their allies are represented by one or two species of Pacific salmon, genus *Oncorhynchus*, from the Klamath River basin of Oregon and the Thompson River of British Columbia, but this genus has not yet been identified from deposits older than the Pleistocene. The genus *Salmo* (of which a Miocene species has recently been described by La Rivers, 1964) is represented by the cutthroat (*S. clarki*) in Lahontan and possibly in Bonneville deposits of Nevada and Utah, the Atlantic salmon(?) (*S. salar?*) in Quebec, and an extinct species, *S. copei* Uyeno and Miller (1963)—formerly *Rhabdofario lacustris Cope*—from Plio-Pleistocene lake beds in southern Idaho. As suggested by Nordón (1961, p. 749) on osteological grounds and here supported by its relatively early fossil appearance, *Salmo* is probably close to the basal ancestor of its subfamily (the Salmoninae). The lake trout (*Salvelinus namaycush*) has been recorded from interglacial clays that perhaps represent the Yarmouth interglacial at Menomonie, Wisconsin. The Bonneville cisco of Bear Lake, Idaho-Utah (*Prosopium gemmiferum*), has recently been discovered in the late-Wisconsin Bonneville terrace of Pluvial Lake Bonneville near Salt Lake City (Stokes *et al.*, 1964); this find constitutes the first fossil record for *Prosopium*.

Esocidae. Among the pikes, only the muskellunge (*Esox masquinongy*) has been definitely identified from Pleistocene deposits, in Texas, Oklahoma, and Kansas, but fossils probably referable to another species (*E. americanus* or *E. niger*) have been reported from Texas.

Cyprinidae. As expected, the ubiquitous minnows, which are of Asiatic origin, have the largest number (24) of fossil species, and not all of those recovered have yet been identified (see, *e.g.*, Smith, 1958: 178). Three genera (*Diastichus*, *Mylocyprinus*, and *Sigmopharyngodon*) and nine species are extinct, all but one of which lived in the "Idaho Lake," discussed later. Seven of the 14 genera, representing 17 species, are from western United States; the remainder are from Saskatchewan, Kansas, Oklahoma, and Texas.

The genus *Gila*, as here broadly interpreted, appears earliest in the record and contains the most fossil species. Two subgenera are recognized and may be distinguished by the number of pharyngeal tooth rows: 2 in *Gila* and 1 in *Siphateles*. The genus includes generalized forms, such as the living Utah chub (*Gila atraria*), also known as fossil

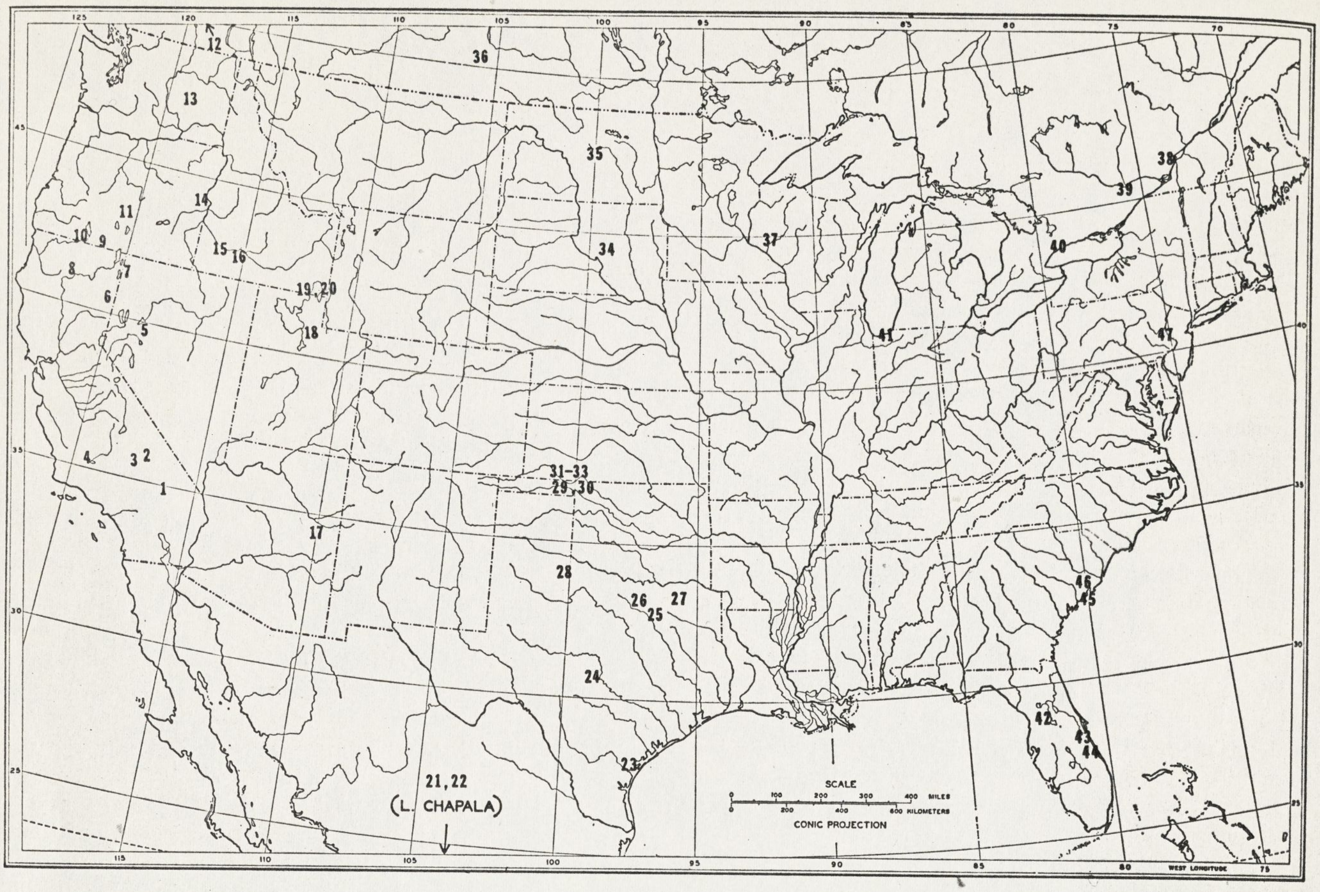


Figure 1. Late-Pliocene and Pleistocene sites for American freshwater fishes. The locations of Plio-Pleistocene and Pleistocene sites where fishes have been recovered in North America are shown by number on Figure 1 and in the list that follows. Following the name of the locality is the probable age, according to these abbreviations: (Int) = Interval of Late Pliocene to Early Pleistocene in southern Idaho and Oregon, (K) = Kansan, (Y) $\doteq$ Yarmouth, (I) = Illinoian, (LI) = Late Illinoian, (P) = Pleistocene, (EP) = Early Pleistocene, (MP) = Middle Pleistocene, (LP) = Late Pleistocene, (S) = Sangamon, (LS) = Late Sangamon, (W) = Wisconsin, (EW) = Early Wisconsin, (MW) = Middle Wisconsin, and (LW) = Late Wisconsin. Radiocarbon datings are given where available. Age assignments for those sites that contain both mammals and fishes are as given by Hibbard *et al.* (this volume). Key references to the literature are indicated for each locality. For certain localities that lack published information, the site is identified in appropriate detail. Three sites, 12 (in Canada) and 21-22 (in Mexico), could not be plotted but are indicated on the map.

(Stokes *et al.*, 1964), and the Mio-Pliocene *Gila turneri*. The nearest Old World relative of *Gila* may be *Tribolodon*, which lives in Japan. A related genus *Ptychocheilus* is known fossil from the Early Pliocene near Juntura, Oregon (Shotwell, 1963, p. 15) and, as *P. prelucius*, from the Middle Pliocene of northern Arizona (Uyeno and Miller, 1965). The 3 widely distributed living representatives of the genus had evidently evolved by late-Pliocene to early-Pleistocene times, since fossils from deposits of this time appear to be osteologically indistinguishable from the Recent forms.

The query in Table 1 after the number of species attributed to *Mylopharodon* results from the uncertainty (Uyeno and Miller, 1963, p. 13) as to whether "*Leucus*" *condonianus* (Middle Pliocene) is referable to the genus *Mylopharodon*. Similarly, the query after *Notropis* indicates tentative identification to this the most abundant genus of American minnows (over 100 living species).

Catostomidae. The suckers are the second most abundant group in the Pleistocene record. Ten of the 14 species occur in western United States, chiefly in the "Idaho Lake." Only the river carpsucker (*Carpiodes carpio*), a species of buffalo (*Ictiobus*), the white sucker (*Catostomus commersoni*), and the black redhorse (*Moxostoma duquesnei*) have been

Key to Figure 1:

1. Manix Lake (LW: 19,500 ± 500), Howard, 1955; Hubbs *et al.*, 1962
2. Lake Searles (LW: ±11,000), Flint and Gale, 1958
3. White Hills (K), Tedford, R. H., pers. com., 1964, fishes associated with an early Irvingtonian mammal fauna near China Lake, Calif.
4. Lake Tulare (LW or MW), Jordan, 1927; Feth, 1961
5. Lake Lahontan (W), La Rivers, 1962
6. Secret Valley (P?), about 34 km on U.S. Hwy 395 W and N of Litchfield, at NW end of Secret Valley, Lassen Co., Calif. (UM-CALIF-2-63).
7. Duck Valley (P?), sand dune and tufa ridge .5 km NW of jct. of State Hwy 81 and road to SW to Madeline Plains, Washoe Co., Nev. (UM-NEV-5-63).
8. Potter Creek Cave (MP), Stock, 1918
9. Lost River (W), Uyeno and Miller, 1963
10. Lower Klamath Lake (LW), Uyeno and Miller, 1963
11. Fossil Lake (W; Int?), Howard, 1946; Uyeno and Miller, 1963
12. Thompson River (LW), Lindsey, C. C., pers. com., 1964, based on salmon remains in Prov. Mus. Victoria, Cat. No. 470-474, 526, British Columbia.
13. Ringold, Moses Lake (EP or MP), Grolier, M. J., pers. com., 1964, fishes from Moses Lake area, Wash.
14. Willow Creek (Int), Uyeno and Miller, 1963
15. Grand View (Int), Hibbard, 1959; Uyeno, 1961
16. Glenns Ferry (Int: 3.1 m.y. B.P.), Malde and Powers, 1962; Evernden *et al.*, 1964; Miller and Smith, MS
17. Snowflake (EP), Lance, 1960; Miller and Uyeno, MS
18. Lake Bonneville (LW), Stokes *et al.*, 1964
19. Provo formation (LW: 13,900 ± 400 B.P.), Bright, 1963
20. Lake Thatcher (MW: 33,700 — 27,000 B.P.), Bright, 1963
21. Chapala formation (Int), Downs, 1958; Clements, 1963
22. Lago de Chapala (LP), Downs, 1958; Clements, 1963
23. Sinton (EW), Hay, 1926
24. Miller's Cave (LW: 7,200 ± 300 B.P.), Patton, 1963
25. Moore Pit (EW: >37,000 B.P.), Slaughter *et al.*, 1962; Uyeno and Miller, 1962a
26. Clear Creek (MW: 28,840 ± 4,740 B.P.), Slaughter and Ritchie, 1963; Uyeno, 1963
27. Ben Franklin (LW: 12,000 — 9,000 B.P.), Slaughter and Ritchie, 1963; Uyeno, 1963
28. Easley Ranch (EW), Dalquest, 1962
29. Berends (I), Smith, 1954
30. Doby Springs (I), Smith, 1958; Stephens, 1960
31. Butler Spring (I), Smith, 1958; Hibbard and Taylor, 1960
32. Mt. Scott (LI), Smith, 1963
33. Jinglebob (LS), Hibbard, 1955
34. Ree Heights (P), Cope, 1891; Uyeno and Miller, 1963
35. Prophet Mts. (LW), Sherrod, 1963
36. Lillestrom (LW: *ca.* 10,000 B.P.), Uyeno and Miller, 1963
37. Menomonie (Y?), Hussakof, 1916
38. Goose River (P), Lambe, 1904
39. Ottawa Valley (P), Dawson, 1872
40. Don beds (S), Coleman, 1933
41. Lake Michigan (P), Hay, 1923
42. Williston (MP), Hay, 1919; Ray *et al.*, 1963
43. Melbourne (W), Hay, 1927
44. Vero (W), Hay, 1917; Weigel, 1963
45. Young Island (P), Hay, 1923
46. Ashley River (P), Hay, 1923
47. Durham Cave (LP), Leidy, 1889

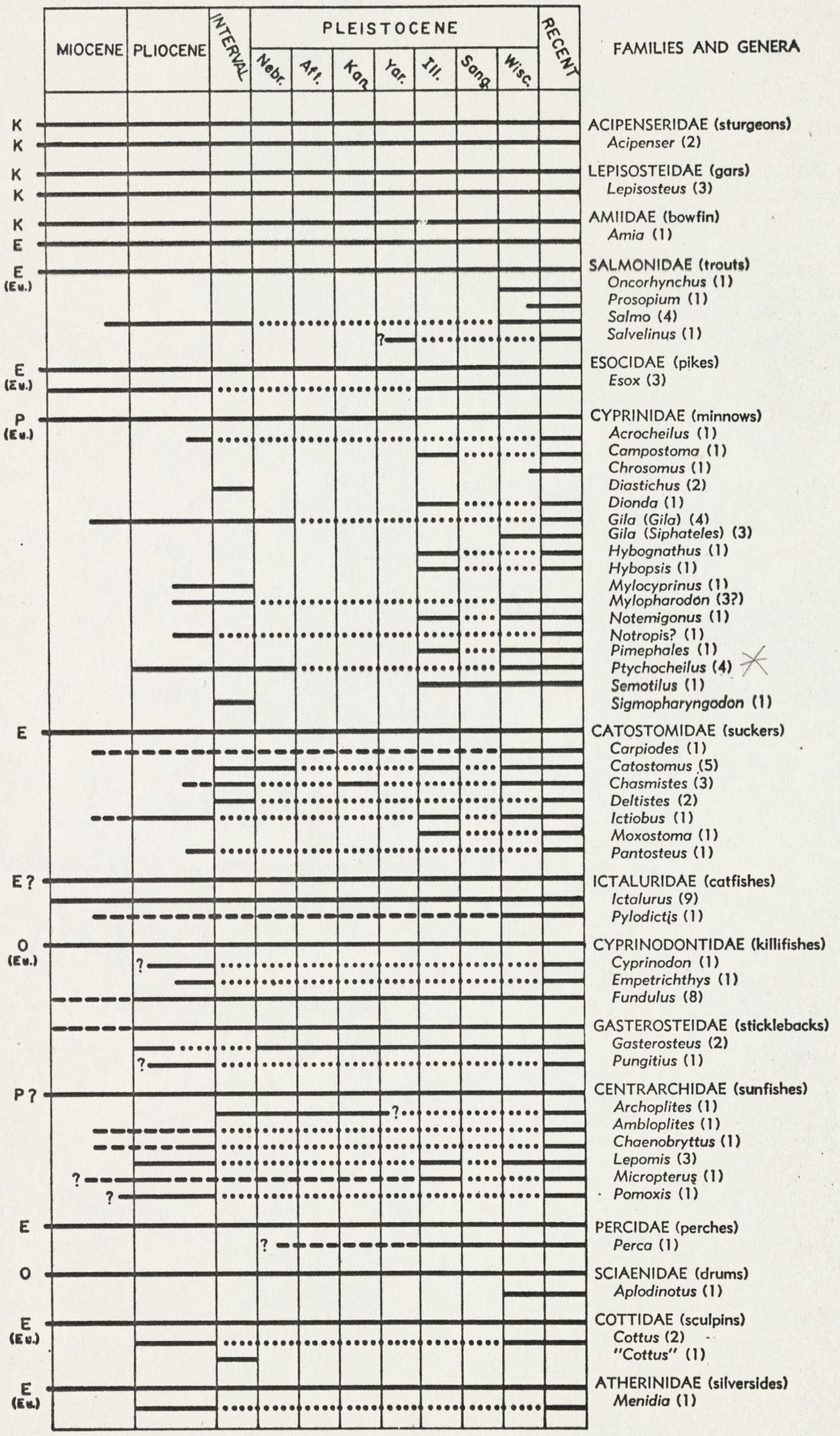
uncovered east of the Rocky Mountains, in North Dakota, Kansas, Oklahoma, and Texas. The distributional significance of the lakesuckers of the genus *Chasmistes*, which now comprises a few relict species, is treated in the section on Paleohydrology.

Ictaluridae. Among the North American freshwater catfishes known as Pleistocene fossils are two bullheads (*Ictalurus melas* and *I. nebulosus*) and the channel catfish (*I. punctatus*) of eastern United States (Uyeno and Miller, 1963, p. 8), an extinct and yet undescribed species of *Ictalurus* from the Plio-Pleistocene "Idaho Lake" (Miller and Smith, MS), and an *Ictalurus* from Lago de Chapala, Mexico, now being described by W. I. Follett. The significance of the former occurrence and extinction of catfish west of the present main range of the family (Fig. 2) is treated in the discussion of the "Idaho Lake" fauna. A fossil record for the large and distinctive flathead catfish (*Pylodictis olivaris*) has only recently been published (Uyeno and Miller, 1962a; the Sangamon age interpretation is now revised to Middle Wisconsin).

Cyprinodontidae. The killifishes, well represented in Pliocene deposits, are definitely known in the Pleistocene by

Table 1

Known Geologic Range of Living Families and Genera of American Freshwater Fishes, Including Four Genera Known Only from the Late-Pliocene to Early-Pleistocene Interval



----- Hypothetical range (see text)
••••••••• Gaps in known fossil record
EARLIEST APPEARANCE: K-Cretaceous; P-Paleocene; E-Eocene; O-Oligocene; Eu-Europe.

Figures in parentheses are the number of species.

only a single species, the banded killifish (*Fundulus diaphanus*), in South Dakota (Uyeno and Miller, 1963, p. 17).

Gasterosteidae. The marine and freshwater stickleback genus *Gasterosteus* is known from Pleistocene beds in the Ottawa Valley of Ontario, Canada.

Centrarchidae. Sunfishes and basses are represented by 5 species in Pleistocene deposits, 3 of which are members of the genus *Lepomis,* the most speciose of living centrarchids. All fossil and Recent records are for eastern United States (the preliminary identification of the "Idaho Lake" sunfish as *Lepomis*—Miller, 1959, p. 194—was wrong; this fossil is an undescribed species of *Archoplites*). The basses of the genus *Micropterus,* regarded by Bailey (1938, p. 77-78) as an early evolutionary development in the family, are known from fragmentary remains in the Early Pliocene of Oklahoma (Laverne formation) and the Late Miocene of Nebraska (Smith, 1962, p. 509; Uyeno and Miller, 1963, p. 10, 23).

Percidae. Perches are represented in the American fossil record only by the yellow perch (*Perca flavescens*) in the Pleistocene of South Dakota, Kansas, and Oklahoma. The abundant and diversified darters, widespread in eastern North America, live largely in habitats poorly suited for fossilization.

Sciaenidae. The freshwater drum (*Aplodinotus grunniens*), an eastern North American species derived from marine forms, is known only from Wisconsin glacial deposits in Michigan and Texas.

Cottidae. The sculpins of the genus *Cottus,* also derived from a predominantly marine family, are known in the Pleistocene thus far only from the late-Wisconsin Bonneville terrace of Utah (Stokes *et al.,* 1964). A related but different and as yet unnamed genus (*"Cottus"* in Table 1), occurs in Plio-Pleistocene beds of the "Idaho Lake" (Uyeno and Miller, 1963, p. 20).

Faunal shifts. Because so few Pleistocene sites have yielded a diversified assemblage of fishes, only limited opportunity exists to demonstrate faunal shifts for these animals. C. L. Smith (1954) described the first diversified Pleistocene fish fauna for North America—the Illinoian Berends fauna of Oklahoma (Fig. 1, Loc. 29), which also includes a variety of mammals and mollusks (Hibbard and Taylor, 1960). The fishes comprise 8 families, 9 genera, and 12 species. By superimposing the ranges of these species where they are presently sympatric it is found that the comparable living fauna occurs from Minnesota to western New York and from the north shore of Lake Huron to central Iowa, central Indiana, and northern Ohio—well to the north of Oklahoma. The inference that the time of the Berends fauna was one of a cooler and moister climate is supported by the present distributional patterns of the associated mollusks and mammals and by the occurrence of spruce, fir, and pine pollen. The yellow perch (*Perca flavescens*) is the fish species that most closely restricts the southern limit of the fauna, for its natural range today lies several hundred miles to the north of northern Oklahoma (Rostlund, 1952, p. 282).

Figure 2. Distribution of the North American freshwater catfishes. Fossil records (X) are indicated for western North America only. (From Miller, 1959, Fig. 5.)

The Mt. Scott local fauna in southwestern Kansas (Fig. 1, Loc. 32), also of Illinoian age, has yielded 14 species of fishes in seven families (Smith, 1963). The majority of these species do not live in the area today. Three of them, the muskellunge (*Esox masquinongy*), brassy minnow (*Hybognathus hankinsoni*), and yellow perch, represent a northern element that occurs today considerably to the north and east of southwestern Kansas. Northern mammals also are associated with the fishes. The inference drawn from the several zoological groups is that the Mt. Scott fauna enjoyed a more extensive aquatic habitat, cooler temperatures, and greater moisture—a climate that is generally similar to that occurring today in southern Wisconsin.

Effects of Pleistocene events. The progressive trend toward increasing aridity and marked seasonal changes associated with the Quaternary has brought about the extinction of some species and sharp restrictions in the ranges of many forms, particularly in the now-arid Great Basin—an area dominated by relict species and populations (Hubbs and Miller, 1948). Withering and desiccation of stream systems and lakes have destroyed aquatic habitats, and the lowering of temperatures during the glacial periods precluded the survival of species whose spawning requirements could not adjust to the new thermal maxima (Miller, 1959, p. 194). On the other hand, glaciation may have also provided the stimulus for the evolution and speciation of such cold-loving genera as the salmons (*Oncorhynchus*) and sculpins (*Cottus*), just as successive lacustrine stages likely triggered the speciation of whitefishes of the genus *Prosopium* in Bear Lake (Idaho-Utah) and the minnows of the subgenus *Siphateles* in the Great Basin. As in other groups of animals, the Pleistocene was a time of diminution of faunas, and the chief changes since then have been largely associated directly or indirectly with man's activities (Miller, 1961; Smith, this volume).

Paleohydrology

Knowledge of both fossil and living fishes may contribute important evidence for the existence of former lakes and streams and of their interrelationships with now-separated drainage systems. On the premise that habitat preferences and ecological tolerances of living species have not changed significantly during the period (chiefly the Pleistocene) when morphology has similarly shown little or no evolution, fossils may also provide information on past climates and paleoecology. Such data supplement and reinforce the interpretations that have been made largely by mammalian and avian paleontologists and, more recently, by students of fossil molluscan faunas (Taylor, 1960a; this volume).

In this section the evidence from the fossil record is integrated with knowledge of the distribution and ecology of existing populations.

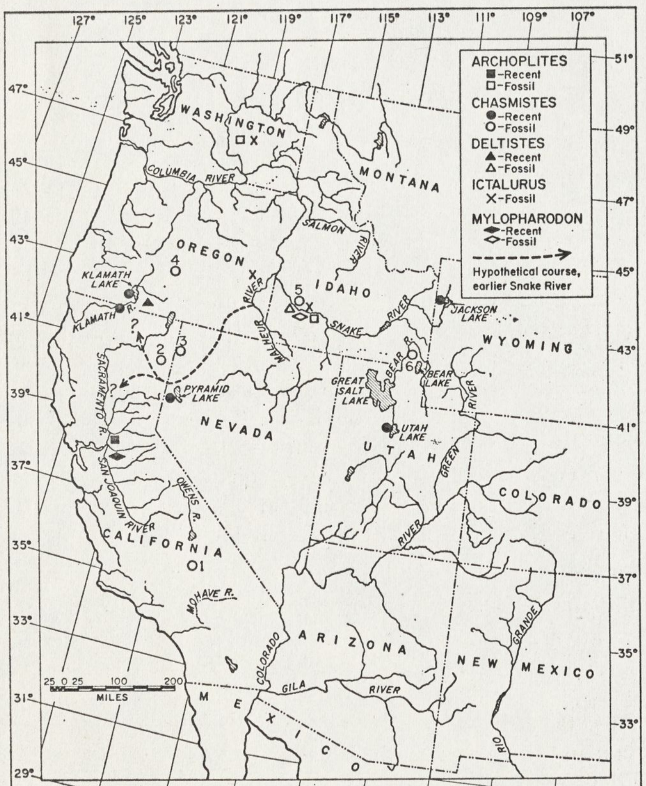


Figure 3. Part of western North America, showing the Recent and fossil distribution of five genera of fishes of the "Idaho Lake" fauna, and the hypothetical course of the Pleistocene Snake River.

The Idaho Lake Fauna

During late-Pliocene time the waters of an earlier Snake River were impounded to create a large Idaho lake in southwestern Idaho and adjacent parts of Oregon (Wheeler and Cook, 1954, Fig. 1; see also Feth, 1961, Fig. 47.1, lake no. 8). This lake, first called the Idaho Pliocene Lake by Cope (1883), evidently persisted into early-Pleistocene times, when it was drained through capture by, or spillover into, the Columbia River basin via the Salmon River. The outlet of Idaho Lake cut the impressive gorge of Hell's Canyon of the present Snake River, along the Oregon-Idaho line (Fig. 3).

The fish fauna of Idaho Lake, as essentially represented in the Plio-Pleistocene Glenns Ferry formation (Malde and Powers, 1962, p. 1206), was first summarized by Cope (1883). Later it was briefly mentioned by Miller (1959, p. 194), and has been studied recently by Uyeno (1961) and by Uyeno and Miller (1963). As now known (Miller and Smith, MS), the fauna comprises 6 families, 15 genera, and at least 20 species, as follows: Salmonidae, *Salmo copei* (formerly *Rhabdofario lacustris*—see Uyeno and Miller, 1963, p. 12); Cyprinidae, 7 or more genera and 10 species, including at least 3 extinct genera (*Diastichus*, *Mylocyprinus*, and *Sigmopharyngodon*) and the first fossil referable to the Columbia River genus *Acrocheilus*; Catostomidae, 4 genera and about 7 species, including the first fossil records for *Deltistes and Pantosteus*; Ictaluridae, 1 species of *Ictalurus*; Centrarchidae, 1 species of *Archpolites,* constituting the first fossil record of this relict Californian genus; and Cottidae, "*Cottus*" *divaricatus* (see Uyeno and Miller, 1963, p. 20). Because the fauna has yet to be studied in detail in its entirety and more material is accumulating, further additions to and modifications of this list may be anticipated.

Excluding such semi-marine types as lampreys, sturgeons, and salmon (*Oncorhynchus*), the fishes living today in this area comprise 4 families, 14 genera, and 21 species—a less diversified assemblage than is represented by the presently known fossil record.

The Idaho Lake fauna is of diverse origin. The trout (*Salmo copei*) is noncommittal, as it is close to the modern cutthroat, *S. clarki*, a species widely distributed today in western North America. Among the minnows is a genus, *Mylopharodon*, restricted today to central California (Sacramento–San Joaquin and Russian River basins—see Fig. 3); the Idaho representative was recently described as distinct from the California species (Uyeno, 1961, p. 338), and a second Idaho species, "*Leucus*" *condonianus*, may pertain to the same genus (Uyeno and Miller, 1963, p. 13). Another Idaho fish that has its nearest living relative in California belongs to the sunfish genus *Archoplites* (Fig. 3), the fossil representative of which is being studied by Miller and Smith (MS). These disjunct sunfishes—of which the Idaho representative seems to have survived in Washington (Fig. 1, Loc. 13) until perhaps the Early or possibly the Middle Pleistocene—represent relicts of a once more widespread distribution of this and other genera of centrarchids (Miller, 1959, p. 199-200).

The genera *Mylopharodon* and *Archoplites* are of particular interest in connection with the pre-Pleistocene waterway between the ancestral Snake River and the Pacific that was hypothesized by Wheeler and Cook (1954, p. 354; see also Fig. 3 herein). At the time they wrote there was no ichthyological evidence to support their view that a river flowed in a southwesterly course via the present lower part of the Malheur River into or near what is now the Klamath or the Sacramento basin of southern Oregon and northern California. Taylor (1960b) reviewed the evidence from the distribution patterns of living mollusks and fishes to support such an independent course of the former Snake River, concluding that the route to the Pacific was by way of the Klamath rather than the Sacramento basin. The present fossil-fish evidence suggests that the history was complex, since neither *Mylopharodon* nor *Archoplites* lives in the Klamath drainage today although other "Idaho Lake" genera occur there now.

The known fossil and present occurrence of the two sucker genera *Chasmistes* and *Deltistes* (Fig. 3) suggests that their distribution—especially that of *Chasmistes*—is likely older than the hypothetical course of the former Snake River, which Taylor concluded was at least as old as Early Pleistocene. The Recent distribution of *Chasmistes* is restricted to six known localities: (1) Snake River near Jackson Lake, Wyoming, based on a specimen at The University of Michigan; (2) Utah Lake, Utah (population extinct); (3) Upper Klamath Lake, Oregon; (4) Lake of the Woods, Oregon (population extinct); (5) Klamath River in Copco Reservoir, California; and (6) Pyramid Lake and, formerly, the adjacent Winnemucca Lake, Nevada. All of these populations, comprising 3 and possibly 5 species (the Lake of the Woods and Snake River samples may represent distinct forms), are usually restricted to lakes during all but the brief spawning period of about two or three weeks; apparently rarely, they may also occur in large rivers. All are large fishes, not infrequently attaining lengths up to 2 ft and weights to 6 lbs (Snyder, 1917, p. 52). The known fossil records clearly demonstrate that *Chasmistes* formerly enjoyed a much wider distribution, extending to the south as far as southern California (Fig. 1, Loc. 3) and inhabiting 5 drainage basins (Death Valley system, Madeline Plains, Duck Flat, Fossil Lake, and Bear River—numbers 1-4 and 6 on Fig. 3), where the genus no longer survives. This distributional pattern, referred to as the "Fishhook Pattern" by D. W. Taylor (personal communication), probably dates back to the Pliocene and indicates that the disjunct localities were formerly connected by a series of rivers and lakes, though they were not necessarily all interconnected with each other at one time.

The minnow subgenus *Siphateles* has similarly correlated past and present distributions (Hubbs and Miller, 1948, p. 79), although fishes of this group have not been identified from Idaho Lake beds (unless critical study of *Diastichus* will show that it represents the phyletic line from which evolved the *Siphateles* division of *Gila*). Other fossil fishes (*Fundulus*, *Empetrichthys*) also demonstrate that waterways connected western Nevada southward to the Death Valley region and westward into southern California probably in late-Miocene or early-Pliocene times (Uyeno and Miller, 1962b, p. 529 and Fig. 7).

Another source for the Idaho Lake fauna and for other beds to the west and north is revealed by the occurrence of fossil catfish of the genus *Ictalurus* (Fig. 3). The family to which this genus belongs is almost exclusively eastern American, with limited crossover to the west of the Continental Divide only in western Mexico (Fig. 2). However, from the Early Pliocene to Early Pleistocene (and possibly around Moses Lake, Washington, into middle-Pleistocene time) *Ictalurus* inhabited southern Idaho, the Juntura basin of adjacent western Oregon, and the middle Columbia basin of Washington (Fig. 3). The area now occupied by the upper Missouri River drainage is the most likely source from which these stocks were derived.

Many other Idaho Lake fishes appear to have been autochthonous—*e.g.* the minnows *Mylocyprinus*, *Sigmopharyngodon*, and *Diastichus*, and possibly the sculpin "*Cottus*" *divaricatus*. Their extinction seems definitely to be correlated with the disappearance of the extensive lacustrine habitat. This seems especially true for the specialized genus *Mylocyprinus*, whose very large and robust pharyngeal bones supported heavy molariform teeth admirably suited for crushing the abundant mollusks that inhabited the lake. The very large molluscan fauna vanished when the lake was drained (Taylor in Uyeno, 1961, p. 334).

Why the squawfish genus *Ptychocheilus*, represented by abundant remains referable to *P. oregonensis* in the Idaho Lake, does not occur in the Klamath system is difficult to explain if the pre-Snake connection was through that basin. This genus has wide ecological tolerance and is probably as old as the early Pliocene (Uyeno and Miller, 1965).

The comparative ages of the fossils associated with the Idaho Lake, their relationships and ecology, and the timing and possible multiple outlets of the pre-Snake drainage will have to be known in much more detail before the fish evidence can be properly appraised.

SPECIATION IN BEAR LAKE

Bear Lake, which crosses the Idaho-Utah line northwest of Great Salt Lake (Fig. 3), is a rather cold and deep oligotrophic body of water, about 20 miles long and 4 to 8 miles wide, with a maximum depth of 208 ft (McConnell *et al.*, 1957). Its relationship to Bear River is unusual in that the river entirely bypasses the lake, entering Bear Valley on the northeastern side and flowing out of the valley directly to the north. At higher lake levels, however, as indicated by old shorelines, Bear River flowed directly into the lake. Detailed knowledge of the geological history of Bear Lake is lacking, but it has been suggested that the valley was occupied by three lakes during Pliocene, early-Pleistocene, and Pluvial times (see Hubbs and Miller, 1948, p. 32).

Four species are endemic to the lake. Three represent whitefishes of the genus *Prosopium:* the Bonneville cisco, *P. gemmiferum*, the Bonneville whitefish, *P. spilonotus*, and the Bear Lake whitefiish, *P. abyssicola*; the fourth is the Bear Lake sculpin, *Cottus extensus*, recently described by Bailey and Bond (1963). The Bonneville cisco was long thought to be a zoogeographical enigma (Hubbs and Miller, 1948, p. 31) because it was classified in the cisco genus *Leucichthys*, a group otherwise largely restricted to eastern North America. Despite its elongate body, projecting lower jaw, and numerous gill rakers—features in which it resembles ciscos—Norden (1961, p. 713) demonstrated that it possesses all of the technical characteristics of the genus *Prosopium*.

Our concern here is with the origin of this species flock in Bear Lake, including an explanation for the coexistence there of a fourth, widely distributed species of the genus *P. williamsoni*. The history of the Bear River and of its associated lakes is critical to the interpretation of this phenomenon and is here summarized from the recent study by Bright (1963). Prior to 34,000 years B.P. (before the present), the Bear River flowed northwestward into the Snake River via the ancestral Portneuf River, near Pocatello, Idaho. Subsequently, but still prior to 34,000 B.P., basaltic lava flows began to obstruct the northern end of the gorge of ancestral Portneuf River near the present town of Soda Springs. Bear River was then gradually forced into a southern course leading into Gentile Valley where it formed Lake Thatcher. Eventually successive lava flows at the northern end of the Thatcher basin built a barrier higher than the lowest rim at the southern end of the lake (elevation 5,445 ft), and Lake Thatcher overflowed into Cache Valley (an arm of Pluvial Lake Bonneville) about 25,000 years B.P. The outlet of Lake Thatcher cut its channel into the resistant rock of Oneida Narrows at least as deep as the present gorge, during which time all of the water from the Bear River basin flowed into Lake Bonneville. Approximately 18,000 years B.P., that lake rose to its highest level, 5,100 ft, and overflowed its barrier at Red Rock Pass to enter Snake River. It then receded to the Provo level.

Thus there were three opportunities for fishes to enter Bear Lake: (1) early in the history of the Bear Valley when Bear River was a direct tributary of the early Snake River; (2) when the connection was first established with Lake Bonneville; and (3) after Lake Bonneville had overflowed into the Snake River. There were also at least three distinct lakes in which ancestral whitefishes could have developed in geographic isolation and later come to coexist in Bear Lake: (1) Bear Lake, (2) Lake Thatcher, and (3) Lake Bonneville. With the exception of Lake Thatcher, these lake basins probably had a long (Pleistocene or earlier) history of successive lake stages.

Prosopium gemmiferum, a small fish seldom more than 7 in. long, is specialized for lacustrine life and is sharply distinct from the other Bear Lake whitefishes in its morphology and habits; it is a filter feeder and spawns at temperatures between 36° and 38° F in late January and early February close to shore and to the bottom. It could have developed either in the Bear Lake or the Bonneville basin; it has recently been discovered in Bonneville deposits (Stokes *et al.*, 1964). *Prosopium abyssicola* is a depwater form, spawning in water 50 to 100 ft deep at temperatures between 35° and 39° F in January and February (or later); it usually lives at depths greater than 75 ft and is a small species, seldom exceeding 9 in. It too could have originated in either the Bonneville or the Bear Lake basin. *Prosopium spilonotus*, the only species caught by anglers, usually spawns over rocky shallows when the water is about 45° F in early December; it is most closely related to *P. williamsoni*, which is scarce in Bear Lake. The latter species is common in larger lakes in the northern part of its range but more frequently inhabits rivers, and all lake populations migrate up inlet streams to spawn on gravel and rubble riffles when the water temperature is about 40° F, from October to early December (Sigler, 1951). Thus all four species are now able to coexist because of differences in feeding habits, spawning time and place, and probably behavioral traits. *Prosopium spilonotus* may have been derived from an early invasion of Bear Valley by *P. williamsoni* or its ancestral form; or it could have developed in Lake Thatcher and have moved into Pluvial Bear Lake when Lake Thatcher was drained by downcutting of its outlet. Further work on the history of the lakes and additional finds of fossil fishes should clarify and will probably modify the interpretation presented here. That the evolution of the three species of *Prosopium* took place during the Quaternary seems probable.

Future Studies

Paleoichthyology has much to offer for the modern investigator since it has now entered a period of stimulating rebirth and is progressing from an isolated discipline to one that is able to contribute to, as well as gain from, the growing fund of knowledge in paleoecology, biogeography, and evolution. Modern technical advances such as dating by radiometric methods are contributing importantly to the promising avenues for future research.

A basic need is to continue studies of the identification and evaluation of fossil remains, using increasingly refined morphological and taxonomic approaches. The nomenclature and classification of numerous groups are very much in need of revision because almost no fossil described twenty years ago can now be taken at face value as properly defined. Studies of new fossil sites and revision of earlier work by the examination of new and better material from known sites are needed and will benefit from the use of multiple, broad-based approaches. Additional comparative studies of the osteology of living forms are essential before the fossil relatives can be properly evaluated. Also critical is the need for comprehensive research on the habits, ecology, and life history of many elements of the existing fish fauna. Close collaboration among paleontologists, geologists, and ichthyologists is required for significant and rapid advances of knowledge in paleoichthyology. Information about changing climates and habitats has the greatest and most lasting significance when a broad spectrum of specialists can exchange data and ideas as they focus their attention on beds of common interest. Such an approach greatly strengthens the contributions from the many special fields.

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Summary

The origin of the freshwater fish fauna of North America scarcely antedates the Cenozoic, except for a few ancient relicts. Fifteen families are represented by 49 genera that are either living today (45) or became extinct near the onset of the Pleistocene. The 49 genera comprise 95 species, of which 5 belong to the 4 extinct genera. In contrast to the 90 species of extant genera that are known as fossil, these same genera are represented by 418 living species. About 60% of the existing fauna may be no older than late Miocene or early Pliocene.

Current knowledge of the occurrence and distribution of North American late-Pliocene and Pleistocene fishes is summarized, and the ecological and evolutionary significance of representatives from the Great Plains and areas west of the Rocky Mountains are discussed. Lacustrine speciation in Bear Lake (Idaho-Utah), relict distributions, and the contribution of the Recent and fossil faunas to paleohydrography in arid Western United States are also treated. Many unpublished data are included.

The first tabular summary of the known geologic range of living families and genera of American freshwater fishes is attempted, along with a map showing late-Pliocene and Pleistocene collection sites. The latter are documented by references.

Most if not all Pleistocene fossils are osteologically indistinguishable from living species. Few sites have sufficiently diversified remains to constitute faunas. Consequently only limited opportunity exists to demonstrate faunal shifts for these animals. As in groups other than fishes, the Pleistocene was a time of diminution of faunas. However, glaciation may have provided the impetus for the evolution and speciation of salmonoids and sculpins (*Cottus*).

The Idaho Lake fauna (Plio-Pleistocene) of southern Idaho is discussed in some detail, although studies of the fish remains are incomplete. The hypothetical former drainage of an earlier Snake River to the Pacific is supported by both fossil and zoogeographic evidence.

Paleoichthyology is now entering a period of challenge, promise, and stimulating rebirth. Much is yet to be learned, however, of the comparative osteology and the habits, ecology, and life history of the living fauna before additional advances can be made in interpreting Quaternary fishes.

Made in United States of America
Reprinted from TRANSACTIONS OF THE AMERICAN FISHERIES SOCIETY
Vol. 98, No. 2, April 1969
pp. 193–208

Life History of the Colorado Squawfish, *Ptychocheilus lucius*, and the Colorado Chub, *Gila robusta*, in the Green River in Dinosaur National Monument, 1964–1966[1]

C. DAVID VANICEK[2] AND ROBERT H. KRAMER[3]
Utah Cooperative Fishery Unit, Utah State University, Logan, Utah

ABSTRACT

Investigations of the ecology and life history of the Colorado squawfish, *Ptychocheilus lucius*, and the Colorado chub, *Gila robusta*, in the Green River in Dinosaur National Monument, Colorado-Utah, were conducted from May 1964, to October 1966. A total of 1,469 squawfish and 2,393 chubs was collected with gill nets, seines, fry gear, and an electric shocker. The operation of Flaming Gorge Reservoir (46 miles above the Monument) has reduced the range of these two species in this area. Age and growth determinations were made from scales from 182 squawfish and 333 chubs. Both species grew slower in years after reservoir operation began (1963–1965) than before (1958–1962); this reduction in growth rate was related to the alteration of seasonal stream-temperature pattern caused by these operations. The bonytail form of the Colorado chub grew faster than the roundtail form. Length-frequency analyses of young squawfish and chubs described seasonal growth of the first three year-classes and provided evidence that these species reproduced successfully in Dinosaur National Monument every year since impoundment, although reproduction apparently did not occur above the mouth of the Yampa River in 1964 and 1966, years of high summer discharge from the dam and resultant lower water temperatures. Time of spawning of the two species varied and was related to water temperature and receding water level. The roundtail and bonytail forms of the Colorado chub had significantly different length-weight relationships. Squawfish over 200 mm total length were entirely piscivorous, while shorter squawfish consumed microcrustaceans and aquatic insects. The diet of the Colorado chub consisted largely of aquatic and terrestrial insects.

INTRODUCTION

Little is known about the life history of the Colorado squawfish, *Ptychocheilus lucius*, or the Colorado chub, *Gila robusta*, both large minnows, which are endemic in the Colorado River drainage (La Rivers, 1962; Sigler and Miller, 1963). The squawfish is the largest native minnow in North America, and has been reported to have reached sizes of 36 kg (80 lbs) and larger. Both species are decreasing in abundance in their native ranges because of man's modification of rivers (Miller, 1961; Minckley and Deacon, 1968) and the squawfish has been placed on the Bureau of Sport Fisheries and Wildlife's list of "Rare and Endangered Fish and Wildlife Species of the United States."

In September 1962, just prior to the closure of the Flaming Gorge Dam (Figure 1), the Green River and its tributaries from Pinedale, Wyoming, to a point 7 miles above the dam site, were treated with rotenone to eradicate non-game fish populations preparatory to the establishment of a sport fishery in the new Flaming Gorge Reservoir and its tailwaters (Binns *et al.*, 1964). Following closure of the dam in November 1962, approximately 90 miles of the Green River

[1] This paper is based on materials prepared for a thesis submitted to the Graduate School, Utah State University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] Present Address: Department of Biological Sciences, Sacramento State College, Sacramento, California 95819.

[3] Unit Leader, Bureau Sport Fisheries and Wildlife.

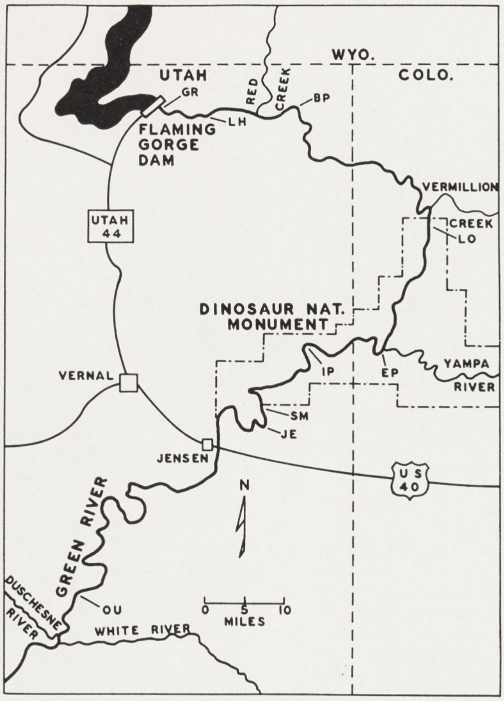

FIGURE 1.—Green River study area, showing location of sampling stations. GR = Greendale (USGS); LH = Little Hole; BP = Bridgeport; LO = Lodore; EP = Echo Park; IP = Island Park; SM = Split Mountain; JE = Jensen (USGS); OU = Ouray.

have been inundated, and operation of Flaming Gorge Reservoir has resulted in major changes in flow and temperature patterns in the river below the dam.[4]

The present investigation was part of a follow-up study to determine the effects of the fish control program upon fish populations in Dinosaur National Monument, 46 miles downstream from Flaming Gorge Dam, and to assess changes on habitat and populations in the Monument brought about by the closure of Flaming Gorge Dam.

METHODS AND MATERIALS

The study area was limited to the Green River primarily in Dinosaur National Monument, but collecting sites were also located above and below the Monument. Location of sampling sites was dictated largely by vehicle and boat access to the river. Intensive sampling stations were established at Lodore, Echo Park, Island Park, and Split Mountain, all within Dinosaur National Monument, and supplemental stations were located at Little Hole, Bridgeport, and Ouray (Figure 1). Fish populations were sampled with nylon experimental gill nets 75- and 150-ft long with mesh sizes ranging from 3/4-inch to 3-inch stretch measure; a 30-ft, 1/4-inch mesh, nylon straight seine; a 15-ft, 1/8-inch bobbinet straight seine; an electric shocker powered by a 230-volt generator and mounted on an 18-ft aluminum flat-bottomed boat fitted with stainless steel electrodes; tow nets; food strainers; and a modified scoop shovel with window-screen inserts.

Fish specimens were preserved in 10-percent formalin in the field and later transferred to 40-percent isopropyl alcohol in the laboratory. Total length (from the tip of the snout to the tip of the caudal fin when compressed) of all fish was measured to the nearest millimeter, and weight was recorded in grams. Approximately 10 scales were taken from the right side of each fish just above the lateral line for age and growth determinations. Stomachs were taken from fish of all size groups, and contents were analyzed with the aid of a binocular microscope.

Continuous recordings of water temperatures were made with Ryan Model D portable recording thermometers. Daily temperature readings were made at all stations with a pocket thermometer when fish samples were taken. Water temperature records were also obtained from U.S. Geological Survey records for gaging stations at Greendale and Jensen. Water quality analyses were made at least once each visit to a sampling station.

Two morphological variants of the Colorado chub were present in the area and are referred to in this study as the "roundtail" and the "bonytail." These two forms were classified as subspecies *Gila robusta robusta* and *G. r. elegans,* respectively, by Miller (1946). The taxonomy of these fishes is poorly understood and criteria are not available for distinguishing between young fish of

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[4] Vanicek, C. David, Robert H. Kramer, and the late Donald R. Franklin (MS). Distribution of Green River fishes following closure of Flaming Gorge Dam.

TABLE 1.—*Mean monthly and annual Green River discharge (cubic feet per second) before and after impoundment, Greendale (compiled from U. S. Geological Survey data)*

Month	Before impoundment (1951–1962) Mean	Range	After impoundment 1963	1964	1965	1966
October	920	573– 1,608	777	128	2,583	1,279
November	814	576– 1,338	900	312	2,343	2,024
December	628	323– 988	268	743	3,151	1,881
January	597	391– 814	367	949	3,506	1,164
February	792	442– 1,503	467	966	3,838	1,293
March	1,413	709– 2,434	106	599	3,782	1,152
April	2,752	1,274– 6,288	134	587	3,420	2,171
May	4,462	1,278– 6,614	130	1,477	1,078	1,352
June	6,996	3,227–11,420	125	1,466	1,439	1,590
July	3,375	909– 6,995	104	2,441	474	1,692
August	1,635	700– 3,711	102	1,992	497	1,921
September	913	643– 1,640	113	2,200	734	2,078
Annual mean[1]	2,102	1,032– 3,226	231	1,555	2,227	1,633

[1] Calculated for "water-years" which begin on October 1 of the preceding calendar-year.

the two morphological variants. Consequently, specimens shorter than 200 mm total length were combined in the present study under the general taxon, Colorado chub. All other names of fishes were taken from those listed by the American Fisheries Society (1960).

PHYSICAL AND CHEMICAL CHARACTERISTICS

Before completion of Flaming Gorge Dam, Green River flow entering Dinosaur National Monument was lowest during winter months and increased gradually until peak run-off in June (Table 1). Following peak run-off, flow receded during the summer and was uniformly low during fall months. Since completion of Flaming Gorge Dam, the annual discharge pattern of the Green River has been greatly altered. The characteristic high spring and low winter flows have been replaced by a relatively stabilized seasonal discharge pattern. Below the mouth of the Yampa River, the Green River has been altered less because the Yampa waters modify the dam's impact, and the seasonal flow pattern resembles that of preimpoundment years.

Before impoundment, yearly water temperature patterns were similar at Greendale and Jensen; temperatures began rising from winter lows of 33 F in March and reached a mean of about 72 F in July (Table 2). In late August, temperatures began a steady decline to winter lows in December. Since dam closure, water temperatures at Greendale showed little seasonal fluctuation and remained largely in the 35–50 F range. Below the mouth of the Yampa River, post-impoundment seasonal temperature resembled the pre-impoundment pattern, although post-impoundment temperatures were slightly lower

TABLE 2.—*Mean monthly Green River water temperatures (°F), before and after impoundment, Greendale and Jensen, Utah (compiled from USGS data)*

Month	Greendale: Before impoundment 1957–59	Greendale: After impoundment 1963	1964	1965	1966	Jensen: Before impoundment 1957–59; 1962	Jensen: After impoundment 1963	1964	1965	1966
January	33	36	41	41	45	33	32	32	–	32
February	33	35	37	38	41	33	33	32	36	–
March	36	36	38	39	39	36	43	35	39	–
April	45	36	40	40	39	48	49	48	45	49
May	52	39	41	42	39	56	59	56	54	58
June	60	41	42	46	40	64	66	61	60	62
July	70	43	45	49	41	72	72	66	67	68
August	68	44	47	50	43	70	72	64	66	64
September	60	42	48	51	44	64	66	59	57	58
October	50	43	54	53	–	50	–	53	54	–
November	35	58	53	53	–	38	42	–	47	–
December	33	48	46	49	–	34	32	–	37	–

in the summer months and higher in the winter months than before impoundment. During the 4 years since closure of the dam, the degree of influence of the dam on downstream water temperatures has varied considerably (Figure 2; Table 2). In years of low summer discharge, 1963 and 1965, summer water temperatures at all Green River locations from Bridgeport downstream to the Yampa River approximated pre-impoundment temperatures. In years of relatively high summer discharge, 1964 and 1966, water temperatures were considerably below those of 1963, 1965, and the pre-impoundment years as far downstream as Island Park and Jensen (Figure 2; Table 2).

Dissolved oxygen concentrations throughout the study area ranged from 6.4 to 8.5 ppm. Total alkalinity, due largely to the presence of bicarbonates, ranged from 65 ppm at spring run-off to 160 ppm in late summer, and pH values ranged from 7.8 to 8.6.

Water discharged from Flaming Gorge Dam was clear and nearly sediment-free, but tributaries downstream discharged heavy silt loads into the river during spring run-off and after heavy showers. Turbidity was highest (up to 5,000 Jackson Turbidity Units) during spring run-off and gradually decreased to less than 100 Units as summer progressed and water level receded.

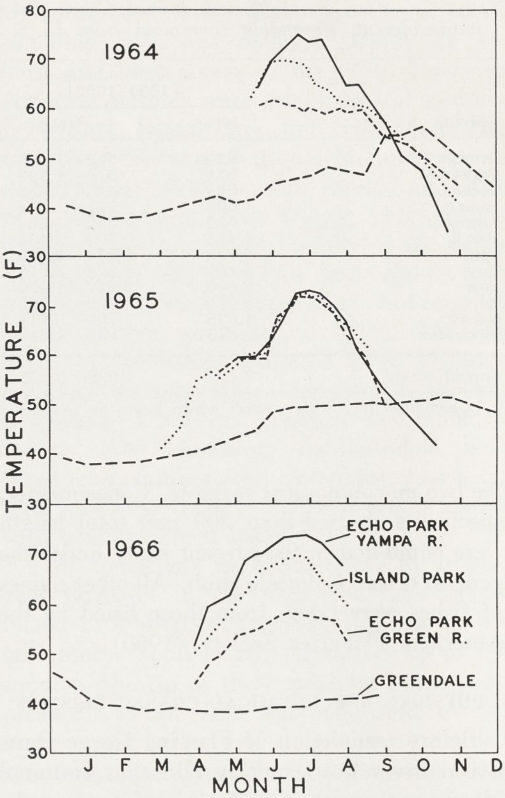

FIGURE 2.—Mean water temperatures at four Green River stations, 1964–1966.

FISH DISTRIBUTION

Colorado squawfish were found from the mouth of the Yampa River downstream to Ouray. This species had been collected between the Yampa mouth and the Flaming Gorge damsite before impoundment, however.[5] Colorado chubs were also commonly found from the Yampa mouth downstream through the Monument, and were occasionally found at Lodore in the present study. They had been present between the damsite and Lodore before impoundment, but were taken above Lodore only in 1963.

Adult squawfish were collected from pools, eddies, and runs, over various bottom types, and were taken with gill nets and the electric shocker. None was found in fast water. Adult Colorado chubs were generally found in pools and eddies in the absence of, although occasionally adjacent to, strong current, and generally over silt or silt-boulder bottom types. These fish were taken by all types of gear, but gill nets were especially effective in capturing larger specimens. No chubs were found in swift water. Young squawfish and chubs were commonly taken in quiet water or shallow pools over silt, sand, and occasionally over gravel bottoms.

Other fish species that were commonly found in Dinosaur National Monument during the present study were the speckled dace, *Rhinichthys osculus;* flannelmouth sucker, *Catostomus latipinnis;* bluehead sucker, *Pantosteus delphinus;* carp, *Cyprinus carpio;* fathead minnow, *Pimephales promelas;* redside shiner, *Richardsonius balteatus;* and channel catfish; *Ictalurus punctatus.*

[5] See footnote 4.

AGE AND GROWTH

The scale method was used to determine age and growth of the Colorado squawfish and the Colorado chub. Five or six scales from each fish were placed between two glass slides, moistened with water, and enlarged 68× with a microprojector similar to that described by Van Oosten, Deason, and Jobes (1934). Annuli were formed in early June on both species. Fish taken before June 1 had not formed an annulus for the current year, but all fish taken after July 1 had formed a new annulus. If a fish had not formed an annulus for the current year, the edge of the scale was recorded as that year's annulus. Scales were not observed on fish shorter than 35 mm total length, and the length at time of scale formation for squawfish and chubs was apparently between 35 and 40 mm. The use of the scale method to determine age and growth was validated for both species by use of the criteria listed by Hile (1941).

Colorado Squawfish

Scale samples from 182 squawfish were analyzed for age and growth determinations. Annuli were recorded from the lateral field of the scale rather than from the more commonly utilized anterior field since circuli in the anterior field were compressed, and annuli were difficult to distinguish. The oldest and largest squawfish taken in this study was an 11-year old female 610 mm long weighing 2268 gms.

The body-scale relationship was linear from a scale radius of 23 mm to about 110 mm; above this length, however, the slope decreased and the relationship was non-linear (Figure 3). Therefore, the relationship was described by two methods. From a scale radius of 23 to 110 mm, a linear regression was fitted by the method of least squares:

$$L = 3.3 + 4.077\ S$$

where L = total body length in millimeters and S = lateral scale radius ×68 in millimeters. For scale radii above 110 mm, a line was fitted by eye. A special nomograph for back-calculating lengths was constructed after Carlander and Smith (1944), which fit the linear relationship up to a scale radius of 110 mm and the non-linear pattern over 110 mm.

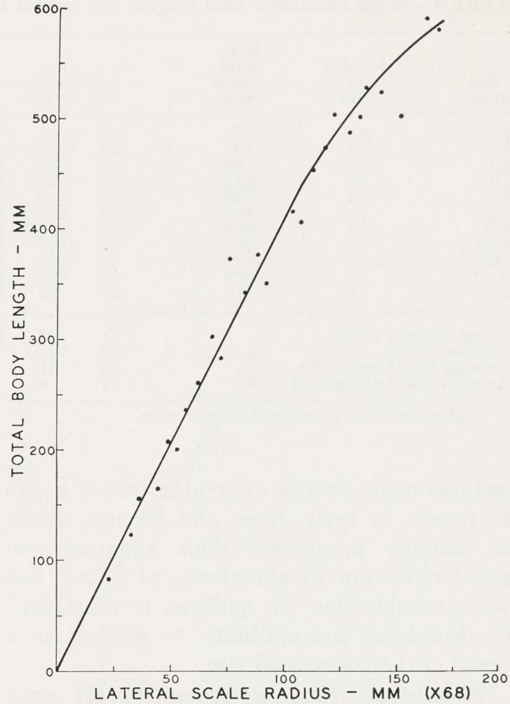

FIGURE 3.—Body-scale relationship of Colorado squawfish, Green River.

Squawfish of all age groups from 0 to XI were included in the age and growth analysis. Mean total length at time of first annulus formation was 44 mm, and average annual increment increased to 73 mm in the fifth year, after which it decreased (Table 3). No difference in growth between sexes was observed.

A "goodness of growth" test, similar to that described by Hile (1941), was performed on age groups I–VIII. Annual variation in growth was expressed as percentage deviation from mean annual increment for the 1958–1965 period, and growth rates decreased steadily (Table 4). In 1958, the annual length increment was 19 percent above the 8-year average, while in 1965, it had decreased to 27 percent below the average.

Within-season growth of age groups 0–II was described. Young-of-the-year squawfish were most numerous in seine collections 3 to 6 weeks after the estimated spawning period, and least common in fall collections. Yearlings were most abundant in seine col-

TABLE 3.—*Mean calculated total lengths and annual increments, Colorado squawfish, Green River, 1964–1966*

Age group	Number of fish	Mean total length (mm)	Mean calculated length (mm) at annulus										
			1	2	3	4	5	6	7	8	9	10	11
I	51	74	43										
II	38	107	40	83									
III	16	168	39	82	136								
IV	16	229	43	92	148	205							
V	16	329	47	78	164	231	298						
VI	16	400	50	110	181	259	325	376					
VII	9	465	47	100	169	252	321	386	432				
VIII	7	505	47	103	176	250	335	402	461	492			
IX	7	537	51	108	165	226	305	382	445	487	523		
X	5	576	54	118	189	273	349	429	487	520	550	568	
XI	1	610	48	99	185	269	372	464	507	532	564	583	600
Grand average length			44	95	162	238	320	391	454	499	536	570	600
Number of fish			182	131	93	77	61	45	29	20	13	6	1
Average length increment			44	51	64	71	73	63	55	35	34	18	17
Average calculated weight (g)[1]			1	6	30	104	260	478	757	1040	1220	1575	1850

[1] Calculated from length-weight regression.

lections made shortly after high waters began to recede in early June, and became scarce as summer progressed. This apparent seasonal reduction in abundance of young fish was probably due (in addition to mortality) to decreasing susceptibility to seining as a result of their increased size.

Fish in all three age-groups (0–II) grew throughout the season, and the length-frequency distributions of these groups clustered about their respective means with no significant overlap (Figure 4). Ages assigned by the length-frequency analyses were in general agreement with the ages and lengths calculated from the scale analyses. Mean length of young-of-the-year fish in late August of 1966 was 24 mm, while in 1964 and 1965, mean lengths at this time were 18 and 15 mm, respectively. This larger size was related to an earlier spawning season in 1966.

Taft and Murphy (1950) reported that the oldest Sacramento squawfish (*P. grandis*) taken in their study from the Sacramento River was 9 years old. The mean calculated standard length at the first annulus was 60 mm and the largest annual growth increment was 80 mm during the second year of life.

The largest northern squawfish (*P. oregonensis*) taken in northern Idaho by Jeppson and Platts (1959) was a 13-year-old female which had a total length of 673 mm and a weight of 4086 gms. Jeppson and Platts also reported that this species grew most rapidly in the second and third years of life, and that the males grew slower than females. Casey (1962) found that the northern squawfish in Cascade Reservoir, Idaho, attained its most rapid growth in its third year, and that growth declined after the sixth year. The oldest fish was 11 years old and 476 mm standard length, but squawfish over 7 years old were rare in Cascade Reservoir.

TABLE 4.—*Percentage deviation from mean annual increment of growth in total length, Colorado squawfish and Colorado chub (roundtail and bonytail forms), Green River, 1958–1965*

Year	Percentage deviation from mean annual increment		
	Squawfish	Roundtail	Bonytail
1958	+19.0	–	–
1959	+12.8	+2.4	+2.7
1960	+15.7	+4.0	+5.9
1961	+ 8.7	+5.8	+0.5
1962	– 2.3	+9.4	+7.0
1963	–11.5	+2.3	–6.1
1964	–15.2	–10.6	–2.2
1965	–27.1	–13.3	–7.6

Colorado Chub

Age and growth determinations of Colorado chubs were based upon scale samples from 333 specimens, including 49 identified as roundtails and 67 as bonytails. Annuli were counted and scale lengths were measured in the anterior field. The largest and oldest roundtail in this study was a 7-year-old female 366 mm long weighing 393 gms. The oldest and largest bonytail was 7 years old, 388 mm long, 422 gms, and of undetermined sex.

The roundtail and bonytail forms of the

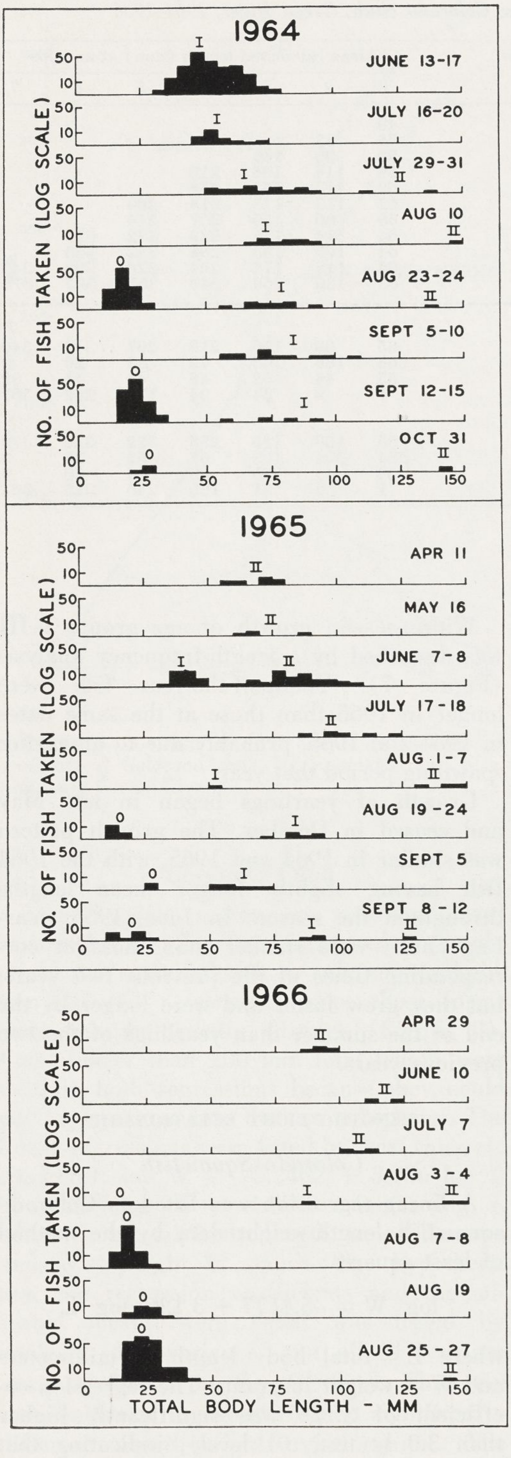

Figure 4.—Length-frequencies of young Colorado squawfish, Green River, 1964, 1965, and 1966.

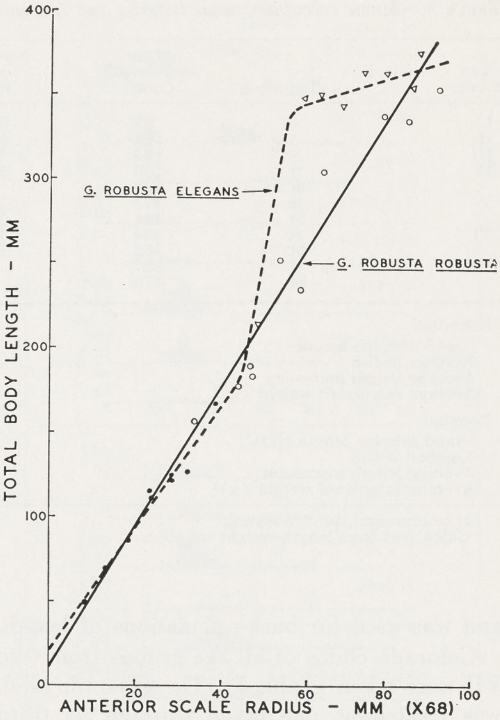

Figure 5.—Body-scale relationship of Colorado chub (*G. r. elegans*-triangles; *G. r. robusta*-open circles; undifferentiated-closed circles), Green River.

Colorado chub had different body-scale relationships and were treated separately. Fish shorter than 200 mm total length were not identified to subspecies and were used in the growth analyses for both subspecies. The roundtail body-scale relationship appeared to be linear (Figure 5) and was described by a linear regression line fitted by least squares:

$$L = 10.5 + 4.12\ S$$

where L = total body length in millimeters, and S = anterior scale radius in millimeters ×68. Lengths at various annuli were back-calculated on a standard nomograph (Carlander and Smith, 1944). The body-scale relationship for the bonytail, however, was non-linear and was described by three straight lines (Figure 5). The lower and upper segments were described by two linear regressions and the middle segment was fitted by eye since data for only one fish was available in this size range. A special nomograph was constructed to fit the S-shaped curve

TABLE 5.—*Mean calculated total lengths and increments, Colorado chub, Green River, 1964–1966*

Age group	Taxon[1]	Mean total length (mm)	Number of fish	Mean calculated length (mm) at annulus						
				1	2	3	4	5	6	7
I	–	65	80	49						
II	–	114	81	51	93					
III	–	165	56	55	96	143				
IV	rt	230	16	59	114	166	210			
	bt	323	5	62	113	153	254			
V	rt	277	13	62	113	173	218	260		
	bt	341	39	63	106	159	237	314		
VI	rt	334	11	64	114	175	229	272	315	
	bt	362	20	64	109	183	288	332	353	
VII	rt	357	9	62	112	172	224	270	308	340
	bt	379	3	63	136	260	349	357	367	373
Roundtail										
Grand average length				55	99	156	218	267	312	340
Number of fish				266	186	105	49	33	20	9
Average length increment				55	44	52	48	44	41	32
Average calculated weight (g)[2]				1	9	34	94	174	282	367
Bonytail										
Grand average length				55	100	158	258	322	355	373
Number of fish				284	204	123	67	62	23	3
Average length increment				55	43	55	89	63	20	6
Average calculated weight (g)[2]				1	8	31	129	240	315	364

[1] rt = roundtail; bt = bonytail.
[2] Calculated from length-weight equation.

and was used for back-calculations of length.

Colorado chubs of all age groups from 0 to VII were taken (Table 5). The Colorado chub was treated as one taxon through its third year of life since fish in this size range could not be classified as either roundtail or bonytail. Above age III the two subspecies were morphologically distinct, and bonytails were longer than roundtails at successive ages (Figure 6). After the third year of life the bonytail grew faster than the roundtail and added its largest length increment during the fourth year after which the increments decreased abruptly. Annual growth increment (length) for the roundtail was greatest during the first year and decreased gradually in the following years. No difference in growth rate in length was observed between sexes. Considerable variability was observed among calculated lengths at the same annulus for both subspecies. A "goodness of growth" test (Hile, 1941) indicated slower growth in post-impoundment years (1963–1965) for both roundtails and bonytails (Table 4). Most rapid growth occurred in 1962 when the percentage deviation from the mean annual increment for the roundtail and bonytail was +9.4 and +7.0, respectively. Poorest growth was in 1965 when percentage deviation for the two forms was –13.3 and –7.6, respectively.

Within-season growth of age groups I–III was described by a length-frequency analysis (Figure 7). Young-of-the-year fish were longer in 1966 than those at the same dates in 1964 and 1965, probably due to an earlier spawning period that year.

Growth of yearlings began in late May and ceased in October. The growth pattern was similar in 1964 and 1965, with the 1964 fish having slightly longer mean lengths throughout the season. In June, 1966, yearling chubs were smaller than those at corresponding times of the previous two years, but they grew faster and were longer by the end of the summer than yearlings of the two previous years.

LENGTH-WEIGHT RELATIONSHIP

Colorado Squawfish

A linear regression was fitted to Colorado squawfish length-weight data by the method of least squares:

$$\log W = -5.4177 + 3.126 \log L$$

where L = total body length in millimeters and W = weight in grams. The regression coefficient of 3.126 was significantly higher than 3.0 (*t* test, .01 level), indicating that the weight of the squawfish increased slightly faster than the cube of its length.

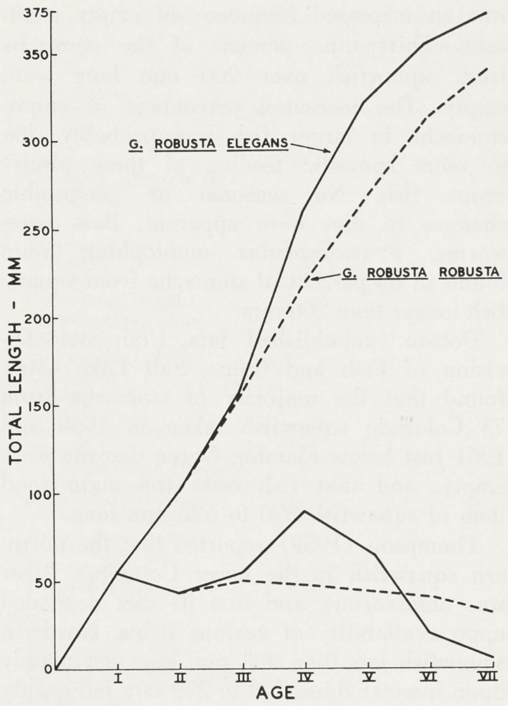

FIGURE 6.—Growth in total length and length increments of Colorado chub (*G. r. elegans* and *G. r. robusta*), Green River.

Colorado Chub

Length-weight regressions were calculated separately for the two forms of Colorado chub, the roundtail (*G. r. robusta*) and the bonytail (*G. r. elegans*) since these forms were morphologically distinct (Figure 8). Fish shorter than 200 mm total length were used in both regressions because they could not be separated into the two subspecies. The linear regressions were fitted by least squares:

roundtail: $\log W = -5.2462 + 3.086 \log L$

bonytail: $\log W = -4.7899 + 2.860 \log L$

where L = total body length in millimeters and W = weight in grams. The hypothesis that the regression coefficients and the adjusted means were equal was tested by analysis of covariance, and all "F" values were significant at the .01 level. Thus the roundtails and the bonytails had significantly different length-weight relationships. The roundtails became heavier than the bonytails as body length increased.

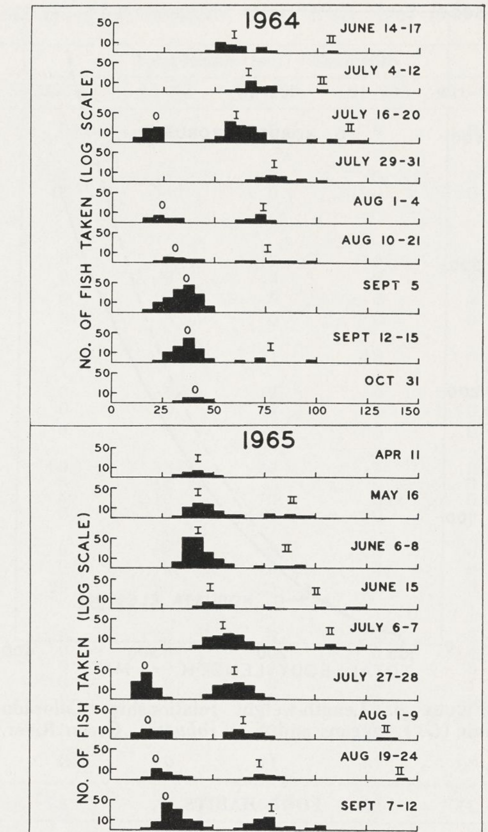

FIGURE 7.—Length-frequencies of young Colorado chubs, Green River, 1964, 1965, and 1966.

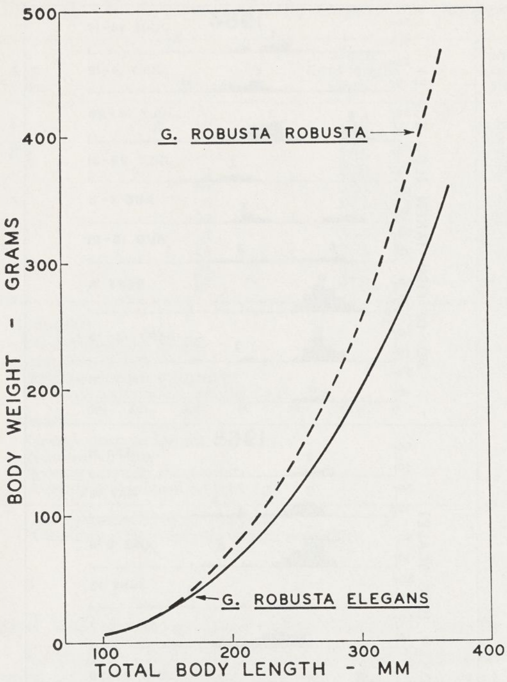

FIGURE 8.—Length-weight relationship, Colorado chub (*G. r. elegans* and *G. r. robusta*), Green River.

FOOD HABITS

Colorado Squawfish

The Colorado squawfish is generally recognized as a carnivore because of its great size, large mouth, and large pharyngeal teeth. It has been reputed to take artificial lures as well as fish, mice, birds, or rabbits as bait (Beckman, 1952), but no detailed food habits studies have been published. Stomachs from 198 squawfish ranging from 15 to 598 mm were analyzed in the present study (Table 6).

Cladocerans, copepods, and chironomid larvae were important food items for squawfish up to 50 mm total length but were not found in larger fish. Utilization of insects increased up to a fish length of 100 mm after which fish became the major food item. Fish were the only food item found in stomachs of squawfish over 200 mm long. The smallest squawfish containing fish was 50 mm in length. The fish species found most often in squawfish stomachs was the redside shiner, but most fish remains were unidentifiable. Concurrent with increased fish utilization was an increased frequency of empty stomachs. Thirty-nine percent of the stomachs from squawfish over 200 mm long were empty. The increased percentage of empty stomachs in larger fish was probably due to more sporadic feeding of these piscivorous fish. No seasonal or geographic changes in diet were apparent. Bass tapeworms, *Proteocephalus ambloplites,* were found in 65 percent of stomachs from squawfish longer than 200 mm.

Dotson (unpublished data, Utah State Division of Fish and Game, Salt Lake City) found that the majority of stomachs from 73 Colorado squawfish taken in 1960 and 1961 just below Flaming Gorge damsite were empty, and that fish were the main food item of squawfish 390 to 628 mm long.

Thompson (1959) reported that the northern squawfish in the lower Columbia River was omnivorous, and that its diet depended upon availability of various items. Northern squawfish less than 203 mm long fed mainly upon insects; those 203 to 279 mm fed mostly on insects and fishes; and those longer than 279 mm fed mostly on fishes and crayfishes.

Colorado Chub

Stomachs from 307 Colorado chubs 15 to 290 mm total length were analyzed (Table 7). Chironomidae larvae and Ephemeroptera nymphs were the most abundant food items in the smaller fish. As they grew, Colorado chubs consumed a greater diversity of food items, including aquatic and terrestrial insects. Principal food items of fish over 200 mm long were terrestrial insects—mostly adult beetles, grasshoppers, and ants—which were commonly found floating on the surface. Chubs were often seen feeding on surface drift material consisting of terrestrial insects and plant debris. Plant debris commonly found in stomachs included leaves, stems, seeds, woody fragments, and horsetail (*Equisetum*) stems.

Fish longer than 200 mm were separated into the two taxa, the roundtail and bonytail. Eight percent of the roundtail stomachs contained fish remains, while no fish remains were found in bonytail stomachs. Colorado chubs shorter than 200 mm containing fish remains were all identified as roundtails.

TABLE 6.—*Percentage occurrence of food items in Colorado squawfish stomachs, Green River, 1964–1966*

Item	Total length (mm)—Squawfish				
	15–25	26–50	51–100	101–200	201–598
Nematodes	0	0	5	0	0
Crustaceans					
Cladocera (*Bosmina* sp.)	27	14	0	0	0
Copepoda	45	14	0	0	0
Insects					
Ephemeroptera					
Nymph	5	0	8	9	0
Adult	0	0	3	9	0
Plecoptera (nymph)	0	0	5	0	0
Thysanoptera (adult)	0	5	0	0	0
Hemiptera					
Corixidae (adult)	0	0	11	18	0
Coleoptera					
Larvae	9	5	2	0	0
Adult	0	0	2	5	0
Trichoptera (larvae)	0	5	3	5	0
Diptera					
Chironomidae (larvae)	60	48	29	5	0
Ceratopogonidae (larvae)	5	14	0	0	0
Unidentified larvae	0	10	3	0	0
Unidentified adult	0	0	2	0	0
Hymenoptera (adult)					
Formicidae	0	0	3	5	0
Unidentified	0	0	2	0	0
Unidentified insects	23	29	23	18	0
Fish					
Cyprinus carpio	0	0	0	0	3
Gila robusta	0	0	0	0	4
Richardsonius balteatus	0	0	2	0	6
Pantosteus delphinus	0	0	0	0	1
Unidentified	0	5	19	36	49
Empty	5	5	13	27	39
Parasitized (Cestoda)	0	0	11	27	65
Total number of stomachs	22	21	62	22	71

Thirty-five percent of the roundtail stomachs examined were empty, while only 11 percent of the bonytail stomachs were empty. The roundtail appeared to be rather opportunistic and sporadic in its feeding habits, taking fish, aquatic insects, and terrestrial insects, while the bonytail fed mainly on terrestrial insects, plant debris, and filamentous algae. No seasonal or geographic differences in diet were indicated. Tapeworms (*Proteocephalus* sp.) were found in 23 percent of stomachs from roundtails over 200 mm, but no tapeworms were found in bonytail stomachs.

McDonald and Dotson (1960) reported that the Colorado chub in the Flaming Gorge Reservoir basin before impoundment was largely omnivorous with its diet including, in order of importance, terrestrial insects, plant matter, and fish.

REPRODUCTION AND YEAR-CLASS STRENGTH

Spawning activities of the two species had not been observed in the Green River and little was known of their reproductive habits in general. Intensive but unsuccessful efforts were made in this study to locate spawning fish and their deposited eggs. Each adult fish collected was examined and was considered to be ripe if eggs or milt were shed when squeezed gently. Relative year-class strengths were estimated from total numbers of fish taken in each year class.

Colorado Squawfish

Time of spawning was indicated by the presence of fish in or near spawning condition in several collections although spawning was not observed nor were eggs located. In 1964, a gravid female (age VII) was taken on August 4. In 1965, one ripe male (age VIII) was taken on August 1. In 1966, three ripe males (ages VIII, IX, and X), one gravid female (age XI), and one spent female (age VII) were collected between June 29 and July 4, and an additional ripe male (age

TABLE 7.—*Percentage occurrence of food items in Colorado chub stomachs, Green River, 1964–1966*

Item	Total length of fish (mm)					
	15–25	26–50	51–100	101–200	201–370	201–390
	Colorado chub[1]				Roundtail	Bonytail
Plant debris	0	2	3	4	27	37
Filamentous algae	5	0	3	4	17	26
Nematodes	5	4	1	1	0	3
Oligochaetes	0	2	0	0	0	0
Arachnids						
Araneae	0	0	0	0	0	3
Hydracarina	0	0	3	2	0	0
Copepods	5	7	0	0	0	0
Insects						
Orthoptera (adult)						
Locustidae	0	2	0	2	10	24
Unidentified	0	0	0	0	8	14
Ephemeroptera						
Adult	0	2	3	4	8	3
Nymph	35	14	4	8	0	3
Plecoptera						
Adult	0	0	1	0	8	3
Nymph	0	0	1	0	0	0
Odonata (adult)	0	0	0	2	0	0
Thysanoptera (adult)	0	2	0	2	0	0
Hemiptera (adult)						
Corixidae	0	0	7	4	8	6
Unidentified	5	5	1	0	0	3
Homoptera (adult)	0	0	1	0	0	11
Megaloptera (larvae)	0	0	1	0	0	0
Coleoptera						
Adult	0	4	5	16	19	31
Larvae	0	4	7	6	0	11
Trichoptera (larvae)	5	5	3	4	0	0
Lepidoptera (adult)	0	0	0	0	0	9
Diptera						
Simuliidae (larvae)	0	0	2	0	0	3
Ceratopogonidae (larvae)	15	2	0	0	0	0
Chironomidae (larvae)	50	21	16	8	0	3
Unidentified larvae	10	0	0	0	0	3
Unidentified adult	0	11	1	2	4	11
Hymenoptera (adult)						
Formicidae	0	7	16	24	17	20
Unidentified	0	0	2	0	8	11
Unidentified insects	60	75	50	32	35	43
Fish (unidentified)	0	0	0	8	8	0
Empty	5	4	16	32	35	11
Parasitized (Cestoda)	0	0	0	0	23	0
Total number of stomachs	20	57	115	50	30	35

[1] Undifferentiated into roundtail or bonytail forms.

VII) was taken on July 20. These fish were found in pools, eddies, and slow runs over boulder or rubble bottoms. Males in spawning condition had many small breeding tubercles on the head. Dotson (unpublished data, Utah State Division of Fish and Game) reported taking ripe male squawfish from the Green River just below the Flaming Gorge damsite on August 3, 1961.

The length-frequency analyses (Figure 4) provided supporting evidence that spawning had occurred during the periods when ripe fish were taken. In all three years, postlarvae 12 to 20 mm long were collected 3 to 4 weeks after the ripe fish were found. Water temperature and receding water level appeared to be important spawning stimuli. The 1966 spawning period was about a month earlier than in 1964 and 1965, and was probably due to the earlier rise in water temperatures (Figure 2) and earlier recession of water level. In all years, ripe squawfish were taken approximately one month after the water temperature had reached 65 F.

Squawfish spawned successfully in the Green River in all 4 years since impoundment, but only below its confluence with the Yampa River. A poor year-class was produced in 1965. Relatively few young-of-the-year (42) were collected that year, and only one yearling was taken in 1966 (Table 8). A weak year-class was also indicated for 1962.

Sex was determined for most fish age V and older. The sex ratio was nearly 1:1 for fish of ages V and VI. After age VI, females became relatively scarce, and 20 of the 24

Table 8.—*Number of Colorado squawfish in 1955–1966 year-classes collected, Green River, 1964–1966*

Year of capture	Year-class											
	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966
1964	3	2	3	4	8	2	7	1	357	275	–	–
1965	2	2	3	3	7	6	14	4	29	53	42	–
1966	1	3	2	2	3	5	2	0	5	8	1	560
Total number taken	6	7	8	9	18	13	23	5	391	336	43	560

fish of age VII and older collected were males. Nearly all squawfish of age VII and older were sexually mature.

Reproduction of the northern squawfish has been studied intensively in northern Idaho. Jeppson and Platts (1959) found spawning occurred in lakes and streams in shallow water over rocks when the water temperature neared 60 F. Keating (1961) reported that squawfish in Cascade Reservoir spawned chiefly over large rubble in riffle areas and at lower ends of pools in tributary streams at temperatures of 60 F and above. Casey (1962) reported that male and female squawfish were sexually mature at ages IV or V, but no males older than age V were found, and females continued to spawn until age XII. Spawning was random over rubble or rock, and each female was attended by several males.

Colorado Chub

Several fish in spawning condition were taken in gill nets, but neither spawning sites nor deposited eggs were located. In 1965, three ripe males and one spent male (ages V–VIII) and two gravid females and one spent female (age VII) were collected. In 1966, six ripe males and two spent females (ages V–VI) were taken. Ripe males had breeding tubercles on their heads and a bright reddish-orange lateral band. All ripe fish were collected in shallow pools and eddies over rubble or boulder bottoms covered with silt. Roundtails and bonytails were taken in spawning condition at the same time of year, but they were never found together in the same gill-net set. Their spawning activities, therefore, may have been spatially separated but concurrent in time. In 1965, six of the seven fish collected in or near spawning condition were roundtails, whereas in 1966, six of the eight fish in this condition were bonytails.

The length-frequency analysis for young-of-the-year fish in 1964 and 1965 (Figure 7) and the presence of gravid and ripe fish in collections suggested that spawning occurred from late June to early July. In 1966, however, the length-frequency analysis (Figure 7) and the presence of ripe fish in the collections indicated that spawning occurred in mid-June. This earlier spawning period was related to the earlier temperature rise and water-level recession. In all years, the suspected spawning period occurred when the water temperature reached approximately 65 F.

The Colorado chub spawned successfully in all 4 years since closure of Flaming Gorge Dam. No evidence of spawning success was found, however, in the Green River above its confluence with the Yampa River in 1964 and 1966. This apparent absence of reproduction was related to lowered water temperatures due to increased discharges from the dam during these 2 years (Figure 2). Water temperatures in the Green River above the mouth of the Yampa were well below 65 F, the suspected threshold temperature for spawning. Colorado chubs apparently reproduced at Lodore in 1965 when temperature patterns were similar to those below the Yampa mouth. Young-of-the-year were collected at Lodore only in 1965, and yearlings were taken there in 1966.

All year-classes since 1957 were represented in the collections (Table 9). Bonytails were more numerous than roundtails for the 1959, 1960, and 1961 year-classes, while the roundtails were more numerous in 1957, 1958, and 1962 year-classes. A particularly abundant year-class of Colorado chubs was produced in 1964.

TABLE 9.—*Number of Colorado chubs in 1957–1966 year-classes collected, Green River, 1964–1966*

Year of capture	Taxon[1]	Year-class 1957	1958	1959	1960	1961	1962	1963	1964	1965	1966
1964	rt	2	3	2	0	0	–	–	–		
	bt	0	1	9	1	0	–	–	–		
	c	2	4	11	1	0	11	257	389		
1965	rt	–	6	4	5	6	–	–	–	–	
	bt	–	2	12	17	3	–	–	–	–	
	c	–	8	16	22	9	12	40	605	269	
1966	rt	–	–	1	4	6	10	–	–	–	–
	bt	–	–	1	7	13	1	–	–	–	–
	c	–	–	2	11	19	11	44	102	152	230
Total number taken	rt	2	9	7	9	12	10	–	–	–	–
	bt	0	3	22	25	16	1	–	–	–	–
	c	2	12	29	34	28	34	341	1096	421	230

[1] rt = roundtail; bt = bonytail; c = combined.

Jonez and Sumner (1954) described the spawning act of Colorado chubs in Lake Mohave. Approximately 500 bonytails were observed spawning over a gravel shelf up to 9 m deep, in May of 1954. Each female had three to five male "escorts." The adhesive eggs were broadcast on the gravel shelf. A gill net in the spawning area caught 42 males and 21 females ranging from 279 to 356 mm (fork length). A 305-mm female contained an estimated 10,000 ripe eggs.

DISCUSSION

The apparent reduction in growth rate of the Colorado squawfish and the Colorado chub from pre- to post-impoundment years may have been a result of lower or higher water temperatures than those before impoundment. During 4 years (1957–1959; 1962) before dam closure, daily mean temperature at the Jensen USGS gaging station was above 60 F for approximately 115 days of the year. Numbers of days with mean water temperature above 60 F in 1963, 1964, and 1965 were, respectively, 147, 103, and 83. Thus, the temperatures of the post-impoundment years may have been less favorable (either too cool or too warm) for growth than were temperatures during pre-impoundment years. Other possible explanations of the apparent reduction in growth rate may have been: 1) survival rate of faster-growing fish was higher than that of slower-growing fish; thus the sample of older fish would be biased toward faster growth during earlier calendar years, or 2) earlier annuli on older fish were missed or incorrectly interpreted.

No consistent relationship between mean annual discharge and year-class strength of squawfish and chubs was apparent. In 1963, the first year after dam closure when flow was extremely low, a particularly abundant year-class of squawfish was produced. Weak year-classes were produced in 1962 and 1965, years of high discharge. In 1964, a year of relatively high discharge, an abundant year-class of chubs was also produced. No exceptionally weak year-classes were indicated for chubs. Estimates of year-class strengths for these years were based upon seine captures of young-of-the-year and juvenile fish, both of which frequent shallow areas and are vulnerable to this method of capture.

The very large squawfish specimens that were found in the Green River in the past have not been reported in recent years, and the largest squawfish taken in this present study weighed 2.3 kg (5 lbs). It is not known whether this apparent absence of large fish is due to reduced growth rate or shorter life span. The complete disappearance of these large fish cannot be assumed since a Vernal, Utah, resident reported to have hooked, but failed to land, a squawfish that he estimated to be approximately 4 ft long in the Green River above the town of Jensen in 1966. Many local fishermen attributed the disappearance of large squawfish to some form of competition with the introduced channel catfish. Several reported observing large dead squawfish containing channel catfish with the spines extended and lodged in the pharynx or esophagus, which probably caused suffocation or starvation. Other possible factors contributing to the apparent reduction in numbers of large squawfish may have been: 1) heavy exploitation of these large fish by local fishermen, since these fish were easily taken by hook and line; or 2) reduction of growth rate caused by heavy parasite loads acquired from predation on introduced fish species carrying exotic parasites.

If the differences in growth, length-weight relationship, and food habits of the roundtail and bonytail forms of the Colorado chub are interpreted as evidence that these forms are distinct entities, perhaps they should be regarded as sibling species rather than subspecies. According to Mayr (1963), a subspecies is an "aggregate of local populations of the species." If two given populations coexist sympatrically without interbreeding, then they are not subspecies, but species. And if they are merely arbitrary segregates within a single interbreeding population, then they cannot be regarded as two subspecies. Thus, reference to the roundtail and the bonytail forms as subspecies would be incorrect since these two forms occur sympatrically in the Green River in Dinosaur National Monument, and both forms were present in the Flaming Gorge Reservoir basin (Smith, 1960). It is not known to what degree these forms occur sympatrically elsewhere in their range, but Jordan (1891) reported collecting both forms from the Gunnison River near Delta, Colorado. The roundtail had been reported to occur mainly in smaller tributaries and in the upper reaches of the main rivers in the Colorado drainage, while the bonytail was thought to have been more restricted to the main channels of larger rivers, downstream from the roundtails (Miller, 1946).

SUMMARY

Investigations to study the life history and ecology of the Colorado squawfish and the Colorado chub in Dinosaur National Monument were conducted from May 1964, to October 1966. Subsequent to initiation of Flaming Gorge Reservoir operations in late 1962, the range of these two species in this area of the Green River has been reduced. No Colorado squawfish were found above Echo Park, 65 miles below the dam, and no Colorado chubs were collected above Lodore, 47 miles below the dam. The squawfish did not show a distinct habitat preference, but the chub showed a distinct preference for pools and eddies.

Age and growth determinations were made from scales from 182 Colorado squawfish and 333 Colorado chubs. Both species grew slower after dam closure (1963–1965) than in pre-impoundment years (1955–1962). This reduction of growth rate was related to the alteration of seasonal temperature patterns caused by operation of the dam. The bonytail form of the Colorado chub grew faster than the roundtail form, while the roundtail became heavier with increase in length than the bonytail.

The squawfish was largely piscivorous, although young squawfish consumed microcrustaceans and aquatic insects. The roundtail and the bonytail differed slightly in their feeding habits. The roundtail was piscivorous and insectivorous, while the bonytail limited its diet to terrestrial insects, plant debris, and algae. Diet of young chubs consisted primarily of aquatic insects.

Time of spawning of Colorado squawfish and Colorado chubs varied and was related to water temperature and receding water level. The Colorado chub spawned when water temperature reached approximately 65 F, and the squawfish spawned approximately 1 month later. Both species reproduced successfully below the mouth of the Yampa River in all 4 years since impoundment.

The environmental requirements of the squawfish and chub are apparently being met in the Green River below its confluence with the Yampa River. However, between Flaming Gorge Dam and Echo Park, the absence of Colorado squawfish and the reduction in range and absence of reproduction in 2 of the last 3 years of the Colorado chub indicates that all environmental requirements, particularly water temperature, are not being met in this stretch of the Green River.

ACKNOWLEDGMENTS

Financial support for this project was provided through the Bureau of Sport Fisheries and Wildlife from funds appropriated under the Colorado River Storage Project Act and from the Utah Cooperative Fishery Unit, a cooperative venture among the Bureau of

Sport Fisheries and Wildlife, Utah State University, and the Utah State Division of Fish and Game. The studies were made under the guidance and field assistance of the late Dr. Donald R. Franklin during the first 2½ years of this project. Appreciation is also expressed to the following agencies and individuals: personnel of the National Park Service (Dinosaur National Monument) and of the Utah State Department of Fish and Game, for providing valuable cooperation in many ways during the study; the U. S. Geological Survey, for readily furnishing unpublished hydrological data; Peter J. Carboni, for field assistance; William D. Pearson and Richard W. Rust, for aid in identification of fish-food items; and Dr. Martin J. Ulmer, for identification of fish parasites.

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THE SOUTHWESTERN NATURALIST 14(3): 297–315 JAN. 15, 1970

DISTRIBUTION OF GREEN RIVER FISHES IN UTAH AND COLORADO FOLLOWING CLOSURE OF FLAMING GORGE DAM[1]

C. DAVID VANICEK

Department of Biological Sciences, Sacramento State College, Sacramento, California

ROBERT H. KRAMER[2] and the late DONALD R. FRANKLIN[3]

Utah Cooperative Fishery Unit, Utah State University, Logan, Utah

ABSTRACT. Flaming Gorge Dam on the Green River, Utah was closed in November, 1962. Studies of fish populations from the dam downstream to Ouray, Utah, were conducted from July, 1963, to October, 1966. The objectives of these studies were: 1) to study changes in river environment associated with closure of the dam; 2) to determine species composition, distribution, and abundance of fishes in the study section; and 3) to compare 1963–1966 distribution of fishes with that reported in pre-impoundment collections. A total of 24,040 fish consisting of 9 indigenous and 12 exotic species was taken in 667 collections by electrofishing gear, gill nets, seines, and fry gear. Flaming Gorge Dam has caused a major change in the ecology of the downstream Green River by alteration of seasonal flows and water-temperature patterns as far as the mouth of the Yampa River, 65 miles below the dam. As a result, native fish populations, particularly in the first 26 miles below the dam, have been largely replaced by introduced rainbow trout *(Salmo gairdneri)*. Below the Yampa River mouth, fish populations were similar to those reported during the pre-impoundment years. During years of high summer discharge from the dam with resultant lower water temperatures (1964 and 1966), no reproduction of any native fishes was found in the Green River above the mouth of the Yampa River.

Flaming Gorge Dam, a unit of the Colorado River Storage Project, was completed in November 1962, by the Bureau of Reclamation. This 455-foot high, arch-type concrete dam is located on the Green River in lower Red Canyon in Ashley National Forest in northeastern Utah. Its primary purposes are generation of hydro-electric power and regulation of river flow. High dams such as this discharge water from lower depths of the reservoir into the tailwaters and often modify the downstream river environment in the following ways: 1) average annual water temperature is lowered, although water temperature may be

[1] Portion of a doctoral dissertation written at Utah State University.
[2] Present Unit Leader, Bureau Sport Fisheries and Wildlife.
[3] Former Unit Leader, Bureau Sport Fisheries and Wildlife.

higher in winter; 2) turbidity is decreased; 3) seasonal extremes in water flow are reduced; and 4) dissolved oxygen concentration is reduced immediately below the dam. These environmental changes may cause a major alteration in fish species composition as has been reported in tail-water areas of large dams by Moffett (1949), Pfitzer (1963), and others.

In September 1962, just prior to the closure of Flaming Gorge Dam, the Green River and its tributaries from Pinedale, Wyoming, to a point 7 miles above the damsite, were treated with rotenone to eradicate the non-game fish population preparatory to the establishment of a sport fishery in the new Flaming Gorge Reservoir and its tailwaters (Binns, *et al.*, 1964). Following closure of the dam in November 1962, approximately 90 miles of the Green River have been inundated, and operation of Flaming Gorge Reservoir has resulted in major changes in flow and temperature patterns in the river below the dam.

This investigation was a part of a follow-up study to determine the effects of the fish-control program upon fish populations in Dinosaur National Monument, 46 miles downstream from Flaming Gorge Dam, and to assess changes on habitat and populations in the Monument brought about by the closing of Flaming Gorge Dam.

The objectives of this specific phase of the follow-up study were: 1) to describe changes in river environment associated with the closure of Flaming Gorge Dam, 2) to determine species composition, distribution, and abundance of fishes in the Green River from Flaming Gorge Dam to Ouray, Utah, after the closure of the dam, and 3) to compare 1963–1966 distribution of fishes with that reported in pre-impoundment collections.

STUDY AREA.—The Green River, the largest tributary of the Colorado River, originates on the western slope of the Wind River Range near the Continental Divide in western Wyoming. It flows southward across a desert plateau into Utah and enters the deep canyons of the eastern Uinta Mountains. After passing into Colorado for a short distance it re-enters Utah and joins the Colorado River in southeastern Utah approximately 730 miles from its source. The drainage area consists of nearly 45,000 square miles of mostly arid or semi-arid land.

The study area extended from Flaming Gorge Dam downstream to the mouth of the White River near Ouray, Utah (Fig. 1). Several tributaries enter the Green River in this 160-mile stretch, but most are intermittent streams which flow mainly during the spring run-off period. The character of the river environment varies considerably in the study area. In Browns Park (between Bridgeport and Lodore) and

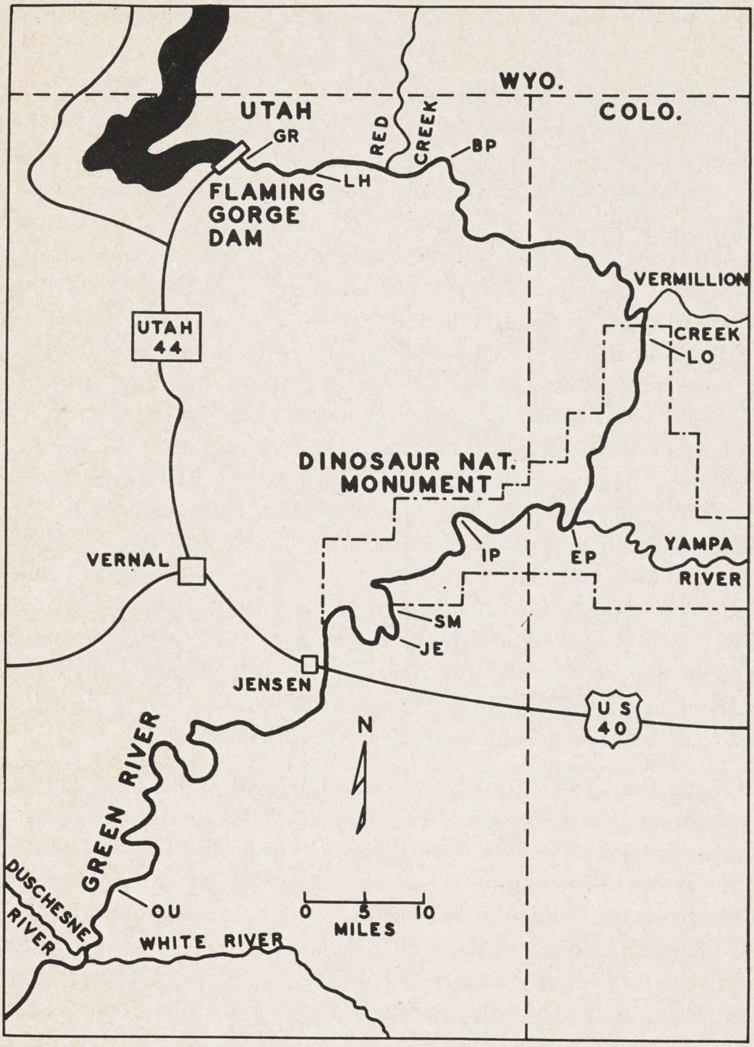

Fig. 1. Green River study area, showing location of sampling stations. GR = Greendale (USGS); LH = Little Hole; BP = Bridgeport; LO = Lodore; EP = Echo Park; IP = Island Park; SM = Split Mountain; JE = Jensen (USGS); OU = Ouray. The Willow Creek sampling station (not shown) is 6 miles below Bridgeport.

below Jensen, the river is slow-flowing with mostly silt and sand bottoms. In Red Canyon immediately below Flaming Gorge Dam and in the canyon areas of Dinosaur National Monument, the gradient is steep and the river is characterized by a diversity of rapids, riffles, eddies, pools, and runs. Bottom substrates are boulder, rubble, sand, and silt.

METHODS AND MATERIALS.—Continuous recordings of water temperature were made at Echo Park and Island Park. Temperature readings were also made at all stations with a pocket thermometer when fish samples were taken. Water quality analyses (dissolved oxygen, alkalinity, conductivity, pH, and turbidity) were made at least once each visit to a sampling station. Water-flow, water temperature, and water-quality data were obtained from the U.S. Geological Survey records for Greendale and Jensen, Utah, gauging stations.

From July, 1963, to October, 1966, 667 collections containing 24,040 fish were made. Most sampling was done from June through September, but several weekend collecting trips were made in April, May, October, and November. Location of sampling sites was limited by vehicle and boat access to the river. Sites for intensive sampling were located at Lodore, Echo Park, Island Park, and Split Mountain. Supplemental sampling stations were located at Little Hole, Bridgeport, Willow Creek, and Ouray (Figure 1). Fish populations were sampled with various types of collecting gear, including gill nets (223 collections), seines of various mesh sizes (264 collections) and a boat-mounted 230-volt a-c electric shocker (121 collections). Tow nets, food strainers, and a modified scoop shovel with window-screen inserts were used to collect larval and small fish (59 collections).

ECOLOGICAL IMPACT OF RESERVOIR OPERATION.—The Green River below Flaming Gorge Dam has changed greatly since the closure of the dam in late 1962. Chemical and physical characteristics of the river immediately below the dam are now dependent upon reservoir conditions at the level of the penstocks and upon the amount of discharge. Downstream from the dam, tributary streams join the river, which gradually attains pre-impoundment conditions. To assess changes caused by the dam, chemical and physical features of the river at increasing distances below the dam before and after impoundment were compared.

Flow.—Before impoundment of the Green River by Flaming Gorge Dam, flow was the lowest during the winter months and increased gradually until peak run-off was reached in May or June. Following peak run-off, the flow receded during the summer months and was uniformly low during the fall months. Since completion of Flaming Gorge Dam, however, characteristic high spring flows and low winter flows have been replaced by a relatively stabilized seasonal flow pattern (Table 1). Monthly and daily flow rates have varied because

TABLE 1

Monthly mean Green River discharge (cubic feet per second) before and after impoundment, Greendale and Jensen, Utah
(compiled from USGS data)

	Greendale						Jensen					
	Before impoundment (1951–1962)		After impoundment (Water year)*				Before impoundment (1951–1962)		After impoundment (Water year)*			
Month	Mean	Range	1963	1964	1965	1966	Mean	Range	1963	1964	1965	1966
October	920	573– 1,608	777	128	2,583	1,279	1,441	883– 2,402	1,112	346	2,737	2,444
November	814	576– 1,338	900	312	2,343	2,024	1,333	932– 1,805	593	632	2,657	2,699
December	628	323– 988	268	743	3,151	1,881	1,005	533– 1,471	528	1,036	3,484	2,584
January	597	391– 814	367	949	3,506	1,164	995	744– 1,304	747	1,199	4,206	1,816
February	792	442– 1,503	467	966	3,838	1,293	1,222	721– 4,676	1,126	1,314	4,448	1,879
March	1,413	709– 2,434	106	599	3,782	1,152	2,590	1,477– 4,435	949	1,023	4,421	3,992
April	2,752	1,274– 6,288	134	587	3,420	2,171	6,513	2,710–15,360	2,029	2,464	6,936	5,415
May	4,462	1,278– 6,416	130	1,477	1,078	1,353	12,159	5,758–23,100	5,507	8,755	9,718	6,799
June	6,996	3,227–11,420	125	1,466	1,439	1,590	13,939	5,575–26,440	3,428	8,172	11,680	4,312
July	3,375	909– 6,995	104	2,441	474	1,692	5,189	1,531–14,740	498	4,189	3,860	2,137
August	1,635	700– 3,711	102	1,992	497	1,921	2,238	724– 4,479	453	2,390	1,686	2,185
September	913	643– 1,640	113	2,200	734	2,078	1,274	645– 2,051	505	2,395	1,829	2,238
Mean	2,102	1,032– 3,226	231	1,555	2,227	1,633	4,179	2,255– 6,230	1,458	2,825	4,797	3,214

* A water year begins on October 1 of the preceding calendar year.

TABLE 2

Monthly mean Green River water temperatures (F), before and after impoundment, Greendale and Jensen, Utah (compiled from USGS data)

	Greendale					Jensen				
	Before impoundment	After impoundment (calendar year)				Before impoundment	After impoundment (calendar year)			
Month	1957–1959	1963	1964	1965	1966	1957–59, 1962	1963	1964	1965	1966
January	33	36	41	41	45	33	32	32	. .	32
February	33	35	37	38	41	33	33	32	36	. .
March	36	36	38	39	39	36	43	35	39	. .
April	45	36	40	40	39	48	49	48	45	49
May	52	39	41	42	39	56	59	56	54	58
June	60	41	42	45	40	64	66	61	60	62
July	70	43	45	49	41	72	72	66	67	68
August	68	44	47	50	43	70	72	64	66	64
September	60	42	48	51	44	64	66	59	57	58
October	50	43	54	53	. .	50	. .	53	54	. .
November	35	58	53	53	. .	38	42	. .	47	. .
December	33	48	46	49	. .	34	32	. .	37	. .

water releases have been dependent upon power demands and downstream water needs. Flows are now less stable on a daily basis but more stable on an annual basis than before impoundment.

Below the mouth of the Yampa River, the flow of the Green River has been altered less because the Yampa waters modify the dam's impact. The seasonal flow pattern at Jensen, about 25 miles below the Yampa's mouth, resembles that of pre-impoundment years. Peak spring-run-off generally occurs in May under present conditions rather than in June as it did before impoundment and it has not reached the mean pre-impoundment peak run-off in the four years since closure of the dam (Table 1). Mean monthly flows in late fall and winter have been higher than before impoundment.

Water Temperature.—Before impoundment, annual water-temperature patterns were similar at Greendale and Jensen (Table 2). Temperatures began rising in March from winter lows of 33°F and reached a mean of about 72°F in July. In late August, temperatures began a steady decline to lows in December.

Since closure of the dam, water temperatures at Greendale have fluctuated little seasonally and have remained in the 35–55 F range because water is discharged from the reservoir's hypolimnion. The rise in temperature to the mid-50 F range observed at Greendale in October or November since impoundment occurred at the time of fall overturn in the reservoir (Eiserman, *et al*, 1967). At Jensen, the post-impoundment seasonal temperature pattern resembled the pre-impoundment pattern, but temperatures after 1962 were slightly lower in the summer months and higher in the winter months than before impoundment (Table 2).

Maximum summer water temperature was inversely related to stream flow. In 1963 and 1965, summer discharges from the dam were relatively low (102–1,439 cfs; Table 1), and water temperatures from Bridgeport downstream to Jensen approximated pre-impoundment conditions (Table 2). The temperatures of the Green and Yampa Rivers were nearly identical at their confluence at Echo Park in 1965 (Figure 2). In 1964 and 1966, however, summer discharges from Flaming Gorge Dam were higher (1,466–2,441 cms; Table 1), and water temperatures were lowered a greater distance downstream. At Echo Park the Yampa River inflow was much warmer than the receiving Green River waters (Figure 2). In these years the Green River at Island Park had warmed considerably (Figure 2) but had not reached pre-impoundment mean temperatures at the end of the study area at Jensen (Table 2).

The inverse relationship between discharge and water temperature was especially apparent at Little Hole and Bridgeport, 7 and 17 miles below the dam, respectively (data from Utah State Department of Fish and Game recording thermometers). During the summers of 1963 and 1965, maximum water temperature at Little Hole was 63 F and 59 F, respectively, while during summers of 1964 and 1966, maximum temperature was 53 F and 55 F. At Bridgeport, maximum summer water temperature in 1963 and 1965 was 76 F and 68 F, respectively, and in 1964 and 1966, 58 F and 60 F.

Water Chemistry.—A comparison of pre-impoundment and post-impoundment water chemistry data from USGS records on mean annual values of bicarbonates, total dissolved solids, specific conductance, and pH at Greendale and Jensen did not reveal any permanent change in these aspects after dam completion (Table 3). In the 1963 water-year, the first year after dam closure, however, the values of bicarbonates, total dissolved solids and specific conductance were much higher than in the other years. These high values were probably the result of the extremely low flow of that year (mean flow = 231 cfs) due to the filling of Flaming Gorge Reservoir. In general, the water chemistry determinations made during the fish collections in the present study gave results similar to those reported by pre-impoundment surveys.

Suspended Sediment and Turbidity.—The Green River at Greendale was nearly sediment-free but increased in silt load progressively

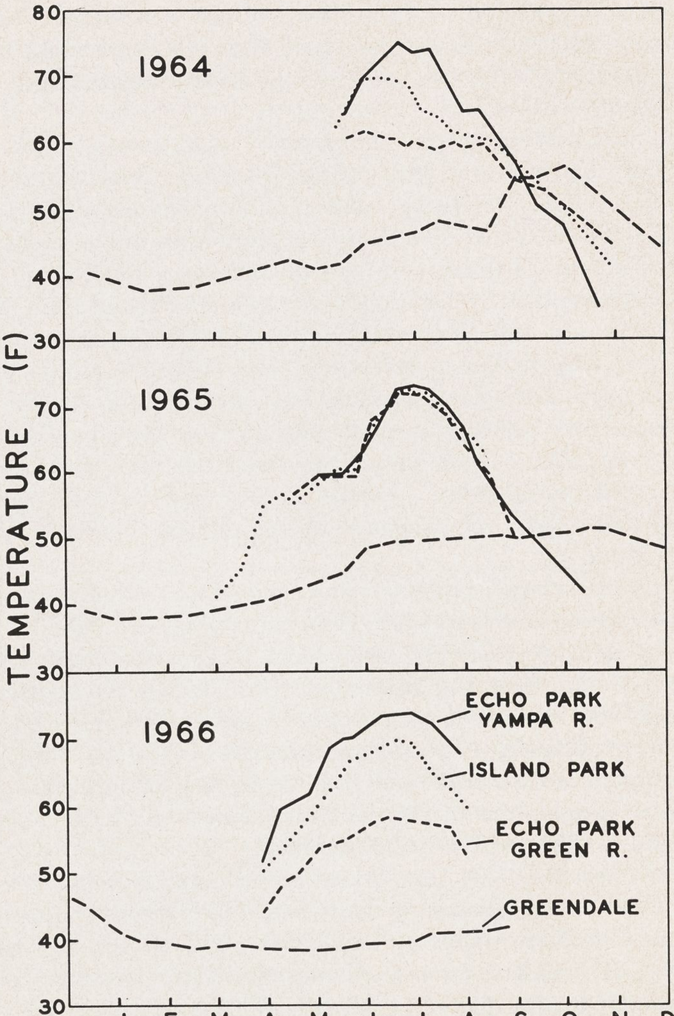

Fig. 2. Mean weekly water temperatures at four Green River stations, 1964–1966.

downstream through the study area. In general, sediment concentration (and turbidity) was highest during spring runoff, immediately after heavy showers, or following increased water releases from the dam. During the 12-year period before closure of Flaming Gorge Dam, mean annual sediment concentration of the Green River at Jensen, Utah, was 1,529 ppm (range: 753–2,430 ppm). After closure of the

TABLE 3

Annual mean discharge and water quality, Green River at Greendale and Jensen, Utah, 1947 to 1966 (compiled from USGS data)

Water year*	Mean discharge (cfs)	HCO_3 (ppm)	Total dissolved solids (ppm)	Specific conductance (micromhos)	pH	Suspended sediment (ppm)
			Greendale			
1956–57	2,877	197	476	705	7.5	...
1957–58	2,430	173	404	624	7.9	...
1958–59	1,576	169	439	662	7.9	...
1959–60	1,375	190	473	716	7.9	...
1960–61	1,032	191	540	784	8.0	...
1961–62	2,919	192	447	685	7.7	...
		Flaming Gorge Dam closed				
1962–63	231	215	653	951	7.8	...
1963–64	1,555	193	465	695	7.7	...
1964–65	2,227	194	551	769	7.8	...
1965–66	1,633	182	536	786	7.9	...
			Jensen			
1947–48	4,215	176	399	617	7.9	...
1948–49	4,708	191	457	709	7.9	1,930
1949–50	5,659	196	479	741	7.6	1,950
1950–51	5,073	186	425	646	7.7	1,220
1951–52	6,230	187	471	700	7.7	2,430
1961–62	6,016	164	333	522	7.7	1,620
		Flaming Gorge Dam closed				
1962–63	1,458	175	526	758	7.6	756
1963–64	2,825	185	408	612	7.7	828
1964–65	4,797	164	371	552	7.6	1,190
1965–66	3,214	165	413	615	7.7	703

* A water year runs from October 1 through September 30 of the following year.

dam, mean sediment concentration was 870 ppm (range: 703–1,190 ppm; Table 3).

Turbidity was measured at each fish collection station and was lowest at Little Hole (less than 25 Jackson Turbidity Units). Highest values were found at Island Park (up to 5,000 JTU).

FISH DISTRIBUTION—POST IMPOUNDMENT (1963–1966). The species composition and relative abundance of fish populations at seven sampling stations between Flaming Gorge Dam and the mouth of the White River were described in the present study (Table 4). Relative abundance of each species was arbitrarily classified as "rare", ocassional

TABLE 4

Occurrence and relative abundance of indigenous and introduced species after closure of Flaming Gorge Dam, 1963–1966 (data from present study)*

	Number collected†	Little Hole	Bridge-port	Willow Creek	Lodore	Echo Park	Island Park	Split Mt.	Ouray
Indigenous species									
Prosopium williamsoni	1	O	O	O	O	R	O	O	O
Gila robusta	2,420	O	O	R	Oc	C	C	C	R
Gila cypha	3	O	O	R‡	O	R	R‡	O	O
Ptychocheilus lucius	1,477	O	O	O	O	Oc	Oc	Oc	Oc
Rhinichthys osculus	3,823	O	R	Oc	C	A	A	A	Oc
Catostomus latipinnis	1,851	R	Oc	Oc	A	A	A	C	Oc
Pantosteus discobolus	1,560	O	Oc	Oc	C	C	C	A	R
Xyrauchen texanus	73	O	O	O	O	Oc	Oc	Oc	Oc
Catostomus × *Xyrauchen*	16	O	O	O	Oc	Oc	Oc	Oc	O
Cottus bairdi	6	O	O	O	O	R	O	O	O
Introduced species									
Salmo trutta	9	O	Oc	O	O	R	O	R	O
Salmo gairdneri	93	A	A	C	C	R	O	O	O
Cyprinus carpio	903	O	Oc	Oc	Oc	Oc	Oc	Oc	A
Gila atraria	1	O	R	O	O	O	O	O	O
Pimephales promelas	2,492	Oc	A	C	C	C	C	C	Oc
Richardsonius balteatus	4,100	R	C	C	C	A	A	C	Oc
Semotilus atromaculatus	12	O	Oc	Oc	O	R	O	R	O
Catostomus commersoni	96	O	O	O	O	Oc	Oc	O	O
Ictalurus punctatus	450	O	R	O	Oc	C	C	C	C
Ictalurus melas	139	O	R	O	O	R	Oc	R	Oc
Lepomis cyanellus	5	O	O	O	O	R	R	R	R
Stizostedion v. vitreum	5	O	O	O	O	R	O	R	R

* O = Not taken; R = Rare; Oc = Occasional; C = Common; A = Abundant.
† Exclusive of larval and post-larval stages for all species except *G. robusta* and *P. lucius*.
‡ Tentative identification.

"~~un~~common", and "abundant", based on total numbers captured (excluding larval and post-larval fishes).

Nine species of indigenous fishes were taken: mountain whitefish, *Prosopium williamsoni* (Girard); Colorado chub[4], *Gila robusta* Baird and Girard; humpback chub, *Gila cypha* Miller; Colorado squawfish, *Ptychocheilus lucius* Girard; speckled dace, *Rhinichthys osculus* (Girard); flannelmouth sucker, *Catostomus latipinnis* Baird and Girard; bluehead sucker, *Pantosteus discobolus* (Cope[5]; humpback

[4] No distinctions were made between the roundtail and bonytail forms of *G. robusta* and they were combined under their common name, Colorado chub (Sigler and Miller, 1963).

[5] Recognized as *Pantosteus delphinus* (Cope) by Bailey *et al.* (1960), and as *Catostomus discobolus* Cope by Smith (1966).

sucker, *Xyrauchen texanus* (Abbott); and mottled sculpin, *Cottus bairdi* Girard. In addition, a hybrid sucker, *Catostomus latipinnis* X *Xyrauchen texanus*, was collected.

Twelve species of exotic fishes were taken: brown trout, *Salmo trutta* Linnaeus; rainbow trout, *Salmo gairdneri* Richardson; carp, *Cyprinus carpio Linnaeus;* Utah chub, *Gila atraria* (Girard); fathead minnow, *Pimephales promelas* Rafinesque; redside shiner, *Richardsonius balteatus* (Richardson); creek chub, *Semotilus atromaculatus* (Mitchill); white sucker, *Catostomus commersoni* (Lacepede); channel catfish, *Ictalurus punctatus* (Rafinesque); black bullhead, *Ictalurus melas* (Rafinesque); green sunfish, *Lepomis cyanellus* Rafinesque; and walleye, *Stizostedion vitreum vitreum* (Mitchell). The occurrence and relative abundance of these indigenous and introduced fishes were described at each of the six major collecting areas.

Little Hole (7 miles below dam).—The only indigenous species occurring in the first 7 miles below the dam was the flannelmouth sucker; one adult specimen was captured and two more were observed (Table 4). Rainbow trout were abundant, while fathead minnows and redside shiners were collected in small numbers. The Colorado chub was reported in the tailwaters of the dam in the summer of 1963, the first summer following impoundment (Rod Stone, Utah Department of Fish and Game, personal interview), but was not taken here in the present study. No reproduction of any fishes was observed in this area.

Bridgeport-Willow Creek (17–23 miles below dam).—The number of species increased considerably at this location, but rainbow trout was still the dominant species. Indigenous species found here were flannelmouth sucker, bluehead sucker, and speckled dace. One Colorado chub and one humpback chub (tentative identification) were collected here in 1963. In addition to the fathead minnow and redside shiner, exotic fishes taken were brown trout (recently stocked by the Utah State Department of Fish and Game), Utah chub, creek chub, and black bullhead. Reproductive success of indigenous fishes was observed here only in 1965 for flannelmouth sucker, bluehead sucker, and speckled dace (Table 5). Exotic species reproducing here in 1965 were fathead minnows and redside shiners. Fathead minnow reproduction was also observed in 1966, but young were found only in a warm, shallow, side-channel that was cut off from the main river.

Lodore (46 miles below dam).—The abundance of Colorado chub, flannelmouth sucker, bluehead sucker, and speckled dace at this station increased from that observed upstream (Table 4). Exotic species commonly found here were rainbow trout, carp, redside shiner, fathead minnow, and channel catfish. The hybrid sucker was collected here and at other stations downstream in Dinosaur National Monument. Morphological characters of this fish were intermediate between the two parental species and agreed with the description by Hubbs and Miller (1953). In 1965, young-of-the-year of the following species were collected: Colorado chub, flannelmouth sucker, bluehead sucker, speckled dace, carp, redside shiner, and fathead minnow (Table 5). In 1964, fathead minnows and redside shiners were observed in spawning condition, but no young-of-the-year were collected.

Echo Park (65 miles below dam).—Species number increased considerably here from that found upstream. Although three distinct sampling stations were recognized at Echo Park (Green River above the mouth of the Yampa River, Green River below the mouth of the Yampa, and Yampa River immediately above its mouth), no major differences in species composition among these three locations were apparent. Three more native species—Colorado squawfish, humpback sucker, and mottled sculpin—were collected in addition to those found upstream (Table 4). In general, the native species were more abundant at Echo Park and at the other two downstream stations in the Monument than at the stations above Echo Park. One humpback chub was collected here in 1963 and was identified by Dr. R. R. Miller as "Apparently representing *Gila cypha*", (letter to Earl M. Semingsen, October 23, 1963). Exotic species taken that were not found upstream in the Green River were white sucker, green sunfish, and walleye. Rainbow trout were still present below the Yampa mouth, but in greatly reduced numbers. One brown trout taken here in 1966 was probably washed out of Jones Hole Creek in a severe flash flood in early July.

Successful reproduction of all native fishes except the humpback sucker was apparent (Table 5). It was not known whether the humpback chub reproduced during these years since the young of this extraordinary fish have not been identified (Miller, 1964). All young-of-the-year and juvenile *Gila* taken in the present study, therefore, were identified as *G. robusta*. Reproduction was also noted for carp, redside shiner, fathead minnow, white sucker, channel catfish, and black bullhead. No reproduction of any species was observed in the Green River immediately above the mouth of the Yampa River in 1964 and 1966.

Island Park (77 miles below dam) *and Split Mountain* (87 miles below dam).—Species composition and relative abundance were very similar to that found at Echo Park (Table 4). One brown trout taken at Split Mountain in 1966 was probably a refugee from the Jones Hole flash flood. Reproduction of all native fishes collected here, except the

TABLE 5

Reproductive success of indigeous fishes at seven locations, Green River, 1964–1966; expressed as presence (X) or absence (O) of young-of-the-year

Species	Little Hole	Bridgeport-Willow Creek	Lodore	Echo Park	Island Park	Split Mt.	Ouray
Gila robusta	O	O	X*	X	X	X	X
Ptychocheilus lucius	O	O	O	X	X	X	X
Rhinichthys osculus	O	X*	X*	X	X	X	X
Catastomus latipinnis	O	X*	X*	X	X	X	X
Pantosteus discobolus	O	X*	X*	X	X	X	X
Xyrauchen texanus	O	O	O	O	O	O	O
Cottus bairdi	O	O	O	X	O	O	O

* 1965 only.

humpback sucker, was observed in 1964, 1965, and 1966 (Table 5). Reproduction also occurred for the following exotic species: carp, fathead minnow, redside shiner, channel catfish and black bullhead.

Ouray (160 miles below dam).—The species composition in this area was different from that found upstream in the Monument. Carp were very abundant, while Colorado chub, speckled dace, flannelmouth sucker, and bluehead sucker, all very common in the Monument, were relatively uncommon. This change in fish populations was probably related to the reduced gradient of the river in this lower area. Young-of-the-year specimens of all native fish species found at this station were collected with the exception of humpback suckers (Table 5). Young-of-the-year carp, fathead minnow, redside shiner, channel catfish, and black bullhead were also collected.

FISH DISTRIBUTION—PRE-IMPOUNDMENT. Data on the pre-impoundment status of Green River fishes within the study are limited and were extracted from five sources:

1) McDonald and Dotson (1960): Investigations by the Utah State Department of Fish and Game, conducted in July and August, 1959, from the reservoir basin to 29 miles downstream from the damsite; gear consisted of gill nets, seines, and primacord;

2) Dotson (unpublished data, Utah State Department of Fish and Game): Fish collected with hook and line by Utah State Department of Fish and Game personnel in August and September, 1960, and August, 1961, in the Flaming Gorge Reservoir basin and immediately below the damsite;

3) Azevedo (Unpublished fishery management report, Bureau Sport Fisheries and Wildlife): Collections from the Green River within

TABLE 6

*Occurrence of indigenous and introduced fish species before the closure of Flaming Gorge Dam, expressed as presence or absence in pre-impoundment surveys**

	Location						
	Little Hole	Bridgeport	Willow Creek	Lodore	Echo Park	Island Park	Split Mt.
Indigenous species							
Gila robusta	1	1	4	4	4,5	4,5	3,5
Ptychocheilus lucius	2	0	0	5	4,5	4,5	3,5
Rhinichthys osculus	1	0	4	4	4,5	4,5	5
Catostomus latipinnis	0	1	4	3,5	4,5	4	3,4
Pantosteus discobolus	0	0	4	4	4,5	4	3,4
Xyrauchen texanus	0	0	4	4	3	0	4
Catostomus × *Xyrauchen*	0	0	0	4	4	0	4
Cottus bairdi	0	0	0	0	0	4	0
Introduced species							
Cyprinus carpio	0	0	1,4	3,4	4,5	4,5	3,4
Pimephales promelas	0	0	4	4	4	0	0
Richardsonius balteatus	0	4	4	4	4	4	4
Ictalurus punctatus	0	1	4	4	4	4	4
Ictalurus melas	0	0	1	0	4	0	4
Stizostedion v. vitreum	0	0	0	0	0	0	3

* 0 = Not reported; 1 = McDonald and Dotson (1960); 2 = Dotson, unpublished data, Utah State Department of Fish and Game; 3 = Azevedo, unpublished fishery management report, Bureau Sport Fisheries and Wildlife; 4 = Banks (1964); and 5 = Binns *et al.* (1964).

Dinosaur National Monument in July and September-October, 1962, using gill nets, fyke nets, rotenone, electrofishing gear, and hook and line;

4) Banks (1964): Collections made by students from Colorado State University from the Green River in Dinosaur National Monument, 1961–1962, using gill nets, seines, rotenone, hook and line, and electrofishing gear;

5) Binns *et al.* (1964): Collection by Utah State Department of Fish and Game personnel in Dinosaur National Monument in September 1962, using seines and electrofishing gear.

Eight indigenous (including one hybrid) and six exotic species were taken in the Green River from the Flaming Gorge damsite downstream through Dinosaur National Monument in these five pre-impoundment collections (Table 6). The indigenous species were Colorado squawfish, Colorado chub, speckled dace, humpback sucker, bluehead sucker, flannelmouth sucker, and mottled sculpin. The hybrid sucker was also reported. The six exotic species collected were carp, fathead minnow, redside shiner, channel catfish, black bullhead, and walleye. These fishes, with the exception of the hybrid sucker and walleye, were all found in Flaming Gorge Reservoir basin (McDonald and Dotson, 1960). Mountain whitefish and humpback chubs were also reported taken from the reservoir basin in 1959 (Gaufin, Smith, and Dotson, 1960).

The collection of humpback chubs in the study area in pre-impoundment years has not been substantiated. Azevedo (unpublished fishery management report, Bureau Sport Fisheries and Wildlife) reported taking two specimens in Split Mountain Canyon on July 23, 1962. Closer examination of these fish by Utah Cooperative Fishery Unit personnel, however, indicated that they were the bonytail form of the Colorado chub. Hagen and Banks (1963) reported collecting two humpback chubs in Echo Park in October 1961, and one specimen at Echo Park on September 17, 1962. In an earlier report, however, Hagen (1962) stated that the identification of the two 1961 fish as humpback chubs was not positive though both had prominent humps and enlarged fins. Banks (1964) included the 1961 and 1962 collections cited above in his thesis, which (for the purpose of the present study) was used as the latest and presumably most accurate analysis of the earlier reports. Apparently subsequent examination revealed that none of the three specimens were humpback chubs because Banks (1964) did not include this species in his lists for the same collections in which they had appeared as cited by Hagen (1962) and Hagen and Banks (1963).

DISCUSSION. A valid comparison between pre- and post-impoundment fish populations is difficult since post-impoundment sampling efforts were much more intensive than the pre-impoundment efforts. In general, species composition in Flaming Gorge Reservoir basin prior to impoundment was very similar to that in Dinosaur National Monument in both pre- and post-impoundment collections. Though few pre-impoundment collections were made from the damsite to Browns Park (26 miles), we made the assumption that the species composition in this area before impoundment was similar to that reported in the reservoir basin before 1963. If this assumption is correct, the most notable changes in species composition is this stretch of river after impoundment have been the disappearance of Colorado squawfish, Colorado chub, humpback chub, and humpback sucker, and the appearance of rainbow trout. Species composition in the river from Browns Park to Echo Park has been altered to a lesser degree, but composition of fish populations is still considerably different from those present at Echo Park.

Fish species composition has not changed in the Green River downstream from its confluence with the Yampa. All native species known to have occurred in Dinosaur National Monument prior to impoundment except the humpback chub, which was never common here, were readily collected from the river in this lower area of the Monument. Several species (in addition to rainbow and brown trout) were collected that were not taken in the five pre-impoundment collections. These were mountain whitefish, Utah chub, creek chub, white sucker, and green sunfish. With the exception of mountain whitefish, these species are ~~not~~ exotics. The occurrence of these fishes probably reflects the more intensive sampling efforts in the present study rather than any change in fish populations. Miller (1964) has reported finding creek chub at Echo Park in 1963 and green sunfish at Island Park in 1962.

The humpback chub, whose taxonomic status needs further study (Smith, 1960), was collected only in 1963, the first year of this investigation. Three specimens were collected. One was taken at Echo Park and was apparently a *bona fide* humpback chub. The other two were extremely humped forms which closely resemble *Gila cypha*. One was taken at Island Park and the other at Swallow Canyon, above Dinosaur National Monument. Little is known of the morphological variability of *G. robusta* or *G. cypha*, and the identification of these two specimens remains tentative.

Although Azevedo (Unpublished fishery management report, Bureau Sport Fisheries and Wildlife), Hagen (1962), and Hagen and Banks (1963) reported taking humpback chubs in Dinosaur National Monument before closure of Flaming Gorge Dam, none of these fish was positively identified. Many of the problems related to the question of the pre-impoundment distribution of the humpback chub will remain unsettled until its taxonomic status is better understood and criteria for positive identification are established. Humpback chubs were listed, however, among the fishes collected by Gaufin, Smith, and Dotson (1960) in the reservoir basin (above the present study area) before impoundment.

On the basis of numbers of fishes taken in the present study, the two most abundant species in the Green River in Dinosaur National Monument were redside shiners and speckled dace, while the species comprising the greatest biomass was the flannelmouth sucker. Smith (1960) reported that the redside shiner was the most common species in Flaming Gorge Reservoir basin prior to impoundment, and that the speckled dace was the most abundant native species.

The primary factor responsible for the major change in the fish fauna in this area was most likely the change in water temperature imposed by the dam. Since impoundment, water temperatures at least as far downstream as Little Hole have not reached the mid-60 F range at which native cyprinids and catostomids spawned below the mouth of the Yampa River. In two of the four summers since impoundment (1964 and 1966), water temperatures in the Green River above the Yampa mouth did not reach this temperature range assumed necessary for spawning, (Vanicek and Kramer, 1969) and no reproduction of any species was observed in this 65-mile stretch of the river proper during these 2 years. The impact of other major environmental changes resulting from closure of the dam, such as alteration of seasonal flow pattern and reduction of turbidity, is unknown. It appears that the long-range ecological changes in the river have now overriden any short-term effects the pre-impoundment fish-control operation may have had on fish populations in the Green River below Flaming Gorge Dam.

CONCLUSIONS. Twenty-one species (9 indigenous, 12 exotic) were collected from the Green River study area in 1963–1966. The rainbow trout was the most abundant species from Flaming Gorge Dam to at least 26 miles downstream; the redside shiner and the speckled dace were the most abundant species in Dinosaur National Monument; and the carp was the most numerous species in the Ouray area below the Monument. The flannelmouth sucker was the most widely distributed fish in the study area, and was especially abundant in the Monument. All species reported in five pre-impoundment surveys were found in post-impoundment years below the confluence of the Green and Yampa Rivers.

The closure of Flaming Gorge Dam in November of 1962 has had a major ecological effect on the Green River downstream by alteration of yearly flow and water temperature patterns. Native fishes have nearly disappeared in at least the first 7 miles below the dam, and a reduction in number of native species has resulted as far downstream as the mouth of the Yampa River (65 miles below Flaming Gorge Dam). Below the Yampa, abundance of indigenous and introduced species apparently has not been affected. High discharges of cold water from the dam reduce the summer water temperature significantly which evidently curtails fish reproduction in the 65-mile stretch of the Green River from Flaming Gorge Dam to the mouth of the Yampa River.

Financial support for this project was provided through the Bureau of Sport Fisheries and Wildlife from funds appropriated under the Colorado River Storage Project Act and from the Utah Cooperative Fishery Unit, a cooperative venture among the Bureau, Utah State Division of Fish and Game, and Utah State University. Gratitude is expressed to personnel of the U.S. National Park Service (Dinosaur National Monument) and of the Utah State Division of Fish and Game, for providing valuable cooperation in many ways; to the U.S. Geological Survey, for willingly furnishing unpublished hydrological data; and to Peter J. Carboni, for field assistance.

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Reprinted from COPEIA, 1970, No. 3, September 3
pp. 409–420

Systematic Studies of the Cyprinid genus *Gila*, in the Upper Colorado River Basin

PAUL B. HOLDEN AND C. B. STALNAKER

Three hundred and nine specimens of *Gila* from the Colorado River basin were studied by taximetrics analysis. Results of the study indicate that the concept of ecosubspecies or ecological subspecies does not fit Colorado basin *Gila*. The roundtail and bonytail chubs, *G. robusta* Baird and Girard and *G. elegans* Baird and Girard respectively, currently treated as subspecies, are well separated morphologically, ecologically, and apparently reproductively and therefore, are better considered two species. The relationship between *G. cypha* Miller, the humpback chub, and *G. elegans* is clouded by the presence of intergrade forms. Future investigations are needed to resolve this problem. Insufficient material was available to make any conclusions on taxonomic status of the Virgin River population. However, the subspecies name *seminuda* Cope and Yarrow should be restricted to *Gila* of Virgin River.

INTRODUCTION

THE cyprinid genus *Gila* is presently divided into three subgenera; *Gila*, *Siphateles* and *Snyderichthys* (Uyeno, 1960). *Richardsonius* is included as another subgenus by some authors (Eddy, 1957). This report is concerned with the systematics of the subgenus *Gila* of the Colorado River basin of western North America with emphasis on forms generally recognized as *G. r. robusta* Baird and Girard, *G. robusta elegans* Baird and Girard, and *G. cypha* Miller (Fig. 1). The following annotated synonymy traces the taxonomic history of these fishes:

Gila robusta elegans—Bonytail chub, widely distributed in Colorado River basin at one time but now reported extinct in lower Colorado basin (Miller and Lowe, 1964; Minckley and Deacon, 1968).

- *Gila elegans* Baird and Girard (1853), Zuñi River, New Mexico. Listed as synonymous with *G. robusta* by Ellis (1914). Placed as a subspecies of *G. robusta* by Miller (1946).
- *Gila emoryi* Baird and Girard (1854), Gila River, Arizona. Listed as *G. emorii* by Jordan and Gilbert (1883). Synonymized by Jordan and Evermann (1896).

Gila robusta robusta—Roundtail chub, widely distributed in Colorado River basin.

- *Gila robusta* Baird and Girard, (1853), Zuñi River, New Mexico.
- *Gila gracilis* Baird and Girard (1853), Zuñi River, New Mexico. Günther (1868) placed *Gila* in genus *Leuciscus* and substituted *L. zunnensis* for *G. gracilis* because *gracilis* was preoccupied in *Leuciscus*. Synonymized by Jordan and Evermann (1896).
- *Gila grahami* Baird and Girard (1854), Rio San Pedro, tributary to Rio Gila, Arizona. Synonymized by Jordan and Evermann (1896).
- *Ptychocheilus vorax* Girard (1857), locality unknown. Synonymized by Jordan and Gilbert (1883).
- *Gila affinis* Abbot (1861), type erroneously ascribed to Kansas River. Synonymized by Jordan and Evermann (1896).
- *Gila nacrea* Cope (1872), tributary of Green River, Fort Bridger, Wyoming. Synonymized by Jordan and Evermann (1896).

Gila cypha—Humpback chub, Colorado River of northern Arizona and southern Utah,

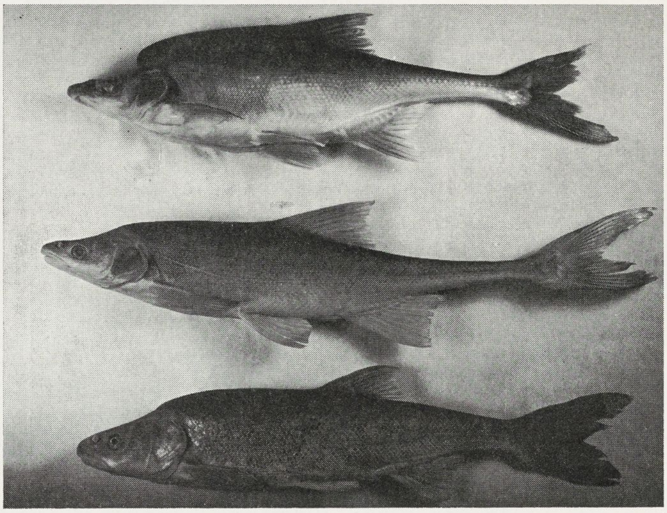

Fig. 1. *Gila cypha, G. elegans,* and *G. r. robusta* from top to bottom.

Green and Yampa rivers of northern Utah and Colorado.

Gila cypha Miller (1946), Grand Canyon of Colorado River, Arizona.

Miller (1946) listed as subspecies of *G. robusta*: *robusta, elegans, seminuda,* and *intermedia*. He indicated they were ecological subspecies, suggesting rapid parallel evolution in disjunct, yet similar, habitats, precluding the idea of a single evolutionary line for each form. This study was undertaken to examine the ecosubspecies concept as applied to Colorado basin *Gila*. Objectives of the study were: to determine systematic relationships between members of the *Gila* complex in the upper Colorado River basin; to determine amount of intraspecific variation exhibited by members of this complex.

Procedures and Methods

Several hundred *Gila* specimens were examined. Of these, 309 specimens ranging in standard length from 159 to 439 mm were intensively studied by taximetrics analysis. Since general body morphology is very different between mature and immature fish, a minimum size of 210 mm standard length was enforced for most fish studied. Specimens were collected primarily by personnel of the Utah Cooperative Fishery Unit, Utah State University, from 1962 to 1967. Additional specimens were graciously loaned by W. L. Minckley, Arizona State University; Ernest Lachner, U. S. National Museum; and John Livesay, Utah State Department of Fish and Game. These specimens represent collections from upper Green River,

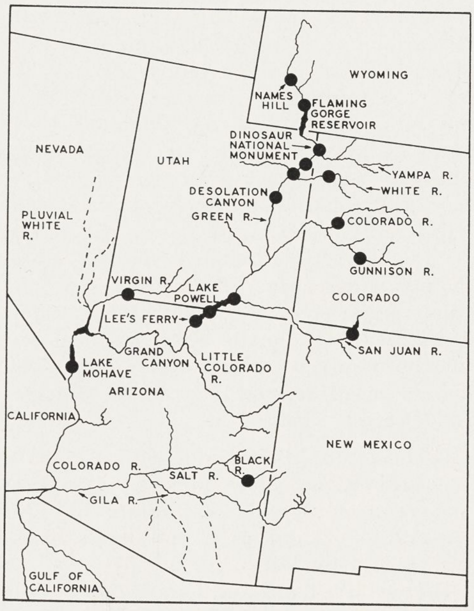

Fig. 2. Map of the Colorado River basin showing areas of fish collections (●) used in this study.

[ca 1970's]

Problems of Coexistence Between Energy Development and the Native Fish Fauna of the Upper Colorado River Basin with a Special Reference to Endangered and Threatened Species

Robert J. Behnke
Department of Fishery and Wildlife Biology
Colorado State University

Introduction

To understand the basic reasons for the endangered and threatened status of some of the fishes native to the Colorado River basin, it is helpful to have some concept of the geologic history of the basin and the long evolutionary history of the species specializing and adapting to an environment which essentially no longer exists. That is, the evolutionary programming resulting in such unusual species as the squawfish, the razorback sucker, the bonytail ahd humpback chubs has dictated life histories and ecologies discordant with present conditions.

The Environment and the Fishes

The Colorado River basin extends approximately 1700 miles from the Gulf of California to the headwaters of the Green River, Wyoming. The present drainage was established when two separate river systems forged a connection by cutting through the present Grand Canyon several million years ago in Pliocene times (McKee, et al. 1967). Except for mainstream species, there has always been a sharp faunistic separation between upper and lower basin fishes (above and below the Grand Canyon). The Colorado River basin probably lacked direct connections with any other major drainage for millions of years. This resulted in long isolation of the fish fauna. Except for species inhabiting headwater streams such as trout, sculpins, speckled dace and mountain suckers, which can be transferred between drainage basins by stream capture, the majority of the native species of the Colorado basin are endemic, that is, they have been so long isolated from their nearest relatives they have evolved into species now restricted to the Colorado basin and found nowhere else. The great antiquity of the native fauna is revealed by chub and squawfish fossils of mid-Pliocene age found in Arizona (Miller, 1958). The Colorado basin fish fauna exhibits the highest degree of endemism of any major drainage in North America. The minnow and sucker families (Cyprinidae and Catostomidae) comprise about 70% of the freshwater fish species native to the Colorado basin. Miller (1958) claimed 87% of the 23 species of minnows and suckers known to be native to the basin at that time are endemic to the basin.

Of the 35+ species of freshwater fishes native to the Colorado River basin, 13 are native to the upper basin. It should be pointed out that a comprehensive, basic ichthyological survey of the upper and lower basins has yet to be made. Long ago, Miller (1946) stressed the need for such a survey.

For example, both the flannelmouth sucker and the bluehead sucker are represented by two morphologically distinct forms. It is not known if these "ecotypes" are reproductively isolated species or local environmental modifications of a common genotype.

The distribution of some of the native upper basin species is disjunct and sporadic. For example, the mountain sucker, Catostomus (Pantosteus) platyrynchus, a typical inhabitant of small tributary streams, is common in such habitat in the Green River drainage of Wyoming, but in Colorado is known only from Piceance Creek (tributary to the White River) and Trout Creek (tributary to the Yampa River). The Piute sculpin, Cottus beldingi, (formerly the Eagle sculpin, C. annae) is known only from a few localities in Colorado, despite an abundance of small, tributary habitat apparently ideal for this species requirements in the basin.

More detailed information on species distribution and faunal associations would be most useful information for interpreting and predicting effects of environmental change and to recognize specific areas where significant numbers of native species yet persist. Holden and Stalnaker (1975) reviewed collections made in the upper basin from 1967 to 1973. Of 29 species found, 19 were non-native fishes.

Prior to the civilizing impact of man, the Colorado River system was characterized by tremendous fluctuations in flow and turbidity. Miller (1961) cites flows recorded in the Colorado River at Yuma, Arizona ranging from 18 cfs in 1934 to 250,000 cfs in 1916. The drainage basin lacked large natural lakes so the native fishes lacked evolutionary specializations for lacustrine environments. There were no barriers to prevent free movement along the main channels and into major tributaries and it is likely migratory movements were a regular part of the life history of the mainstream species.

For millions of years the unique environment of the Colorado River with its great diversity and torrential flows through canyon areas, directed the evolutionary pathways followed by the native fishes and molded the bizarre morphologies of the razorback sucker, the humpback and bonytail chubs and produced the largest of all North American minnows, the giant squawfish.

The major tributaries draining the mountains and foothills formed meandering streams with quiet backwater areas which were likely important reproductive and nursery areas for the native fishes.

The effects of mainstream dams on the large, mainstream species is well known because the dramatic environmental changes can be characterized as sudden and catastrophic in relation to the survival of these species in the new reservoirs or in the cold, clear tailwaters below the dams. Other gradual, cumulative impacts relating to land-use practices have been occurring for more than 100 years in the basin. These more subtle environmental changes are difficult to quantify and the assumption of their negative influence on the presently endangered and threatened species is largely theoretical and circumstantial. Major tributaries such as the Yampa, White, Gunnison and San Juan rivers, following predictable channel development dictated by the principles of fluvial geomorphology would continually cut new channels creating ox-bows of quiet backwater habitat off from the new main channels. It is logical to assume that the utilization of such predictably occurring backwater environments as nursery areas for the young of the main channel fishes (analogous to the importance of estuarine areas for early life history stages of many marine fishes), would be incorporated as an intrinsic part of their life history.

Because of fertility and ease of irrigation, the river bottom lands were the first lands to pass into private ownership. To protect their investments from the natural encroachment of the rivers and to prevent flooding and facilitate irrigation, landowners began to channelize the rivers and rip-rap the banks to better confine and control the rivers' flow. The advent of the bulldozer has greatly accelerated this process.

There is no documentation, to my knowledge, estimating the loss of backwater habitat in the upper basin. Also, there is no documentation in reference to the significance of such habitat in the life history of any of the endangered or threatened species.

The circumstantial evidence of the significance of quiet, backwater environments concerns the frequent field observations of squawfish and particularly razorback suckers in such areas and the appearance of young of both of these species in the Walter Walker Wildlife area near Grand Junction, Colorado in 1975--an artifically created backwater pond resulting from gravel excavation and subsequent innundation by the Colorado River. A population of razorback suckers occurs about 30 miles upstream from Grand Junction, also in an area where a backwater area connects to the Colorado River. Because these backwater habitats are so rapidly vanishing, all existing areas possible associated with any of the endangered and threatened species should be identified and, if possible, protected--at least until we have a better understanding of the significance of such environments.

The example of the backwater pond in the Walter Walker Wildlife area suggests the obvious potential to create more of such environments in an attempt to restore species such as the squawfish and razorback sucker to areas of the upper basin where they no longer exist or are rapidly declining.

The construction of mainstream dams, forming large lakes, regulating flow regimes, precipitating out the silt load and releasing cold, clear water, created new environments for which the native mainstream fishes were ill adapted. The four mainstream specialized species: squawfish, humpback chub, bonytail chub and razorback sucker have suffered catastrophic declines from their former abundance. The razorback sucker has maintained limited populations sporadically throughout its former range, but is particularly rare in the upper basin. The incidence of hybridization between the razorback and flannelmouth suckers is increasing in a changing environment. Such hybrids have long been known (Hubbs and Miller 1953) but 40 of 93 specimens of razorback sucker specimens collected from 1967 to 1973 in the upper basin were found to be hybrids (Holden and Stalnaker 1975). The razorback sucker (_Xyrauchen texanus_) is currently proposed for threatened status under the Endangered Species Act.

The squawfish (_Ptychocheilus lucius_) has not been found in the lower basin since 1968 and has been continually declining in the upper basin. The decline of the squawfish was apparently well underway in the upper basin prior to the construction of Flaming Gorge Reservoir (1962) and Lake Powell (1963). Squawfish were rarely encountered in the pre-impoundment surveys of 1959 and 1960. This earlier decline can be attributed to the gradual, cumulative effects of a changing environment, pollution and a changing fish fauna, becoming increasingly dominated by non-native fishes. A non-native species I would single out as particularly inimical to the squawfish and other native fishes is the redside shiner, Richardsonius balteatus. The redside shiner was first found in the upper Green River, Wyoming in 1938. By 1959 it was the dominant species in the upper Green River drainage as determined by the Flaming Gorge pre-impoundment surveys (Smith 1960, Bosley 1960).

The redside shiner was not found in the Yampa River drainage during a 1952 survey (Baily and Alberti 1952). This species was first recorded from the lower Yampa in 1961 (Banks 1963), was judged as moderately abundant in 1966 samples (Dr. Kent Andrews, personal communication) and was the dominant species in collections made in 1975-76 (Prewitt et. al. 1976). No sign of successful squawfish reproduction (finding young) has been observed in the Yampa River since 1969 (Holden 1973; Prewitt et. al. 1976), and adult specimens continue to deline in fish collections of various surveys made from 1967-1976. The Yampa River has not been altered by large, mainstream dams or any other modification which may be characterized as resulting in sudden and catastrophic change. The decline here is associated with gradual, cumulative changes favoring the introduced species. The squawfish is currently listed as an endangered species under the Endangered Species Act.

The bonytail chub (Gila elegans) was at one time widely distributed and abundant in all the mainstream of the Colorado and Green rivers and major tributaries. Its virtual demise came about rapidly after the construction of large, mainstream dams and is now one of the rarest species in the basin, holding on in small numbers in Lake Mohave in the lower basin and perhaps in the Green River in Desolation Canyon, Utah. I know of no authenticated records of G. elegans from other areas in recent years. The problem of documenting data on the bonytail chub is complicated by the fact that this species has long been confused with the common roundtail chub, G. robusta, and also by the increase in the incidence of hybridization among the Gila chubs (bonytail, humpback and roundtail) since the completion of Lake Powell and Flaming Gorge Reservoir.

The bonytail chub has been proposed for endangered status under the Endangered Species Act.

The humpback chub (Gila cypha) was probably always relatively rare and of local occurrence in deepwater canyon areas of the Colorado and Green rivers. Most of the former prime humpback chub habitat was innundated by the numerous mainstream reservoirs and the few known present populations in the upper basin appear to be affected by hybridization with G. elegans and/or G. robusta. As with the razorback sucker, a changing environment with a preponderance of non-native species has stimulated the breakdown of reproductive isolation and further threatens the existence of the original species.

The humpback chub is recognized as an endangered species under the Enadngered Species Act.

The native cutthroat trout of the upper basin should be considered as threatened. This beautiful fish is virtaully extinct as pure populations. Although also suffering from habitat loss, the major factor in the decline of the native trout has been the introduction of non-native trouts which have replaced or hybridized with the native subspecies.

Energy Development, Coexistence and Realities

Considering the history of extinction of other animal species in relation to the prospects for continued survival of the four endangered and threatened species, it should be recognized that if well-documented curves of historical abundance were available for these species, they would likely be beyond the inflection point where the process of extinction proceeds rapidly toward zero abundance.

Another doleful aspect for the future of the endangered and threatened species is that natural resource and conservation oriented groups and agencies are not likely to make a unified stand to champion the cause of endangered and threatened Colorado River fishes because these species are of the minnow and sucker families and of little direct economic significance. Although the environmental changes, unwise planning, mismanagement of Colorado River water and the fate of the native fishes makes a tragic story, the fact remains that the new reservoirs support multi-million dollar recreational fisheries - based entirely on non-native fishes - and a fishery that was never possible under pristine conditions with the native fishes.

The Endangered Species Act provides some protection of habitat of the species listed, particularly section 7 of the Act which prohibits the activities of any federal agency from jeopardizing the continued existence of these species. However, a mere "holding the line" on preserving what is left of the former environment may not be sufficient to prevent extinction and certainly will not serve to increase the distribution and abundance of these species to a point where they are no longer considered endangered or threatened; these species can be restored only by creating conditions conducive to successful reproduction and survival of early life history stages in areas where such conditions no longer exist.

Because of the above considerations I have come to believe that the most hopeful option for avoiding extinction of species such as the squawfish is for future development projects to build in endangered species mitigation and enhancement plans from the earliest planning stages, analogous to salmon restoration projects on Pacific Coast rivers.

For example, squawfish and razorback suckers have been artificially propagated but the problem of where to stock the young for any survival is yet to be solved. Excavations for dam construction could be made to create artificial backwater areas and to serve as spawning and nursery grounds. Control structures could be designed to exclude non-native competitors and predators. Flow regimes from a dam should attempt to reach a downstream minimum temperature of 68 F by mid-June and maintain a predetermined minimum flow for the reproductive season.

So little is known of the life histories of the endangered and threatened species that there is no assurance that an enhancement project will work or what would be the best project design. But time is running out and to avoid initiating some attempt to perpetuate endangered species, while awaiting the results of years of basic research to learn some subtle aspects of life history and ecology, is a delaying tactic and we may find that although the new information is useful, it is too late.

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THE SOUTHWESTERN NATURALIST 19(4): 403–412   JAN. 20, 1975

DISTRIBUTION OF FISHES IN THE DOLORES AND YAMPA RIVER SYSTEMS OF THE UPPER COLORADO BASIN[1]

PAUL B. HOLDEN AND CLAIR B. STALNAKER

Utah Cooperative Fishery Unit, Utah State University, Logan 84322

ABSTRACT. Fish sampling was conducted in the Dolores River, Colorado, in 1971 and the Yampa River system of Colorado, 1968–71 with emphasis placed on rare and endangered species. Eleven species were found in the Dolores River, but no rare and endangered forms were collected. Twenty-two species were collected in the Yampa River system, including four rare and endangered forms: Colorado squawfish (*Ptychocheilus lucius*), humpback chub (*Gila cypha*) bonytail chub (*Gila elegans*) and humpback sucker (*Xyrauchen texanus*). The Yampa system appeared important to reproduction and preservation of Colorado squawfish.

The native fish fauna of the Colorado River basin represents one of the least understood groups of fishes native to a major North American river basin. Reasons for this are the rugged terrain surrounding the Colorado River and the low economic and sport value placed on these species. The Colorado River has in the last 50 years been greatly desecrated, with much of the system either dry or ponded into great reservoirs. These factors have greatly limited the available habitat for native fishes. Several species are now rare and endangered. Colorado squawfish (*Ptychocheilus lucius*) and humpback chub (*Gila cypha*) are presently considered rare and endangered by the U. S. Department of the Interior (1968). The humpback sucker (*Xyrauchen texanus*) and bonytail chub (*Gila elegans*) are very rare also (Miller 1972).

The native fish of the Colorado River system can be separated into two groups: (1) large river forms found in main channels of the Colorado River, Green River and larger tributaries, and (2) small stream forms found primarily in the lower basin (Nevada, Arizona) in small streams and springs. Minckley and Deacon (1968) reviewed the status of native fishes in the lower Colorado basin (below Grand Canyon). They concluded that large forms are virtually extinct in the lower basin. Therefore, the upper Colorado basin remains the only refuge for these unique fishes. This paper is concerned with the Yampa and

[1] Portion of a doctoral dissertation written at Utah State University.

Dolores river systems and reports on the distribution of fishes with emphasis on rare and endangered species. Alterations in the form of reservoirs have been proposed for both rivers in the near future (U. S. Dept. Interior 1966; U. S. Bur. of Reclamation 1963).

STUDY AREAS. *Dolores Study Area.* The Dolores River (Fig. 1) is a clear, cool stream above Dolores, Colorado with a considerable trout fishery. Immediately below the town, most of the water is taken out for irrigation during summer. The stream then runs at various low flows until it joins the San Miguel River below Uravan, Colorado. The San Miguel is cool, relatively clear and at their confluence has a flow many times greater than the Dolores during the irrigation season. Much of this middle Dolores River below Cahone, Colorado, consists of fairly slow-moving water having pools interspersed with small riffles. At times parts ofthe river appear to dry up completely. Below the mouth of the San Miguel, the stream is characterized by long pools and short rapids. The river carries a very high salt load below its middle stretch.

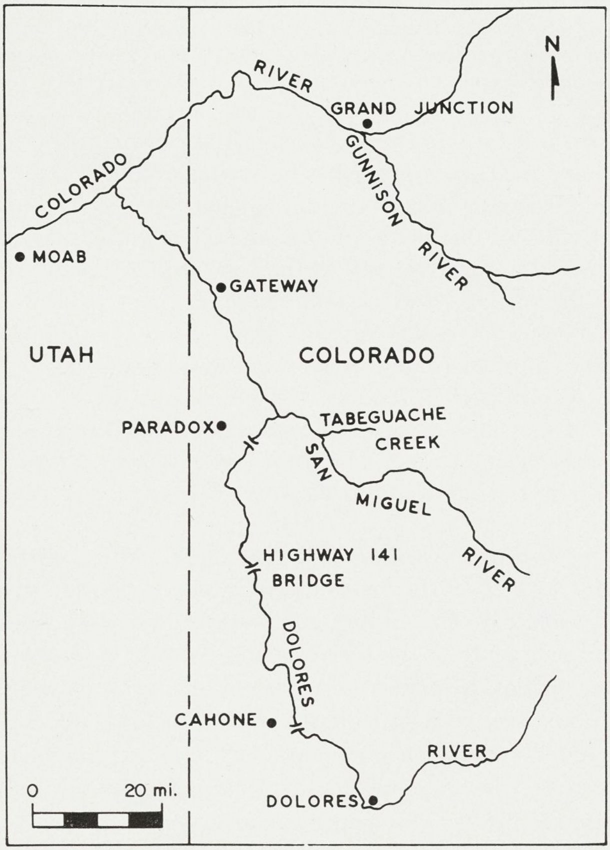

Fig. 1. Map of the Dolores River System.

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Vol. 104, No. 2, April 1975
pp. 217–231

Distribution and Abundance of Mainstream Fishes of the Middle and Upper Colorado River Basins, 1967–1973

PAUL B. HOLDEN AND CLAIR B. STALNAKER

Utah Cooperative Fishery Unit
Logan, Utah

ABSTRACT

Twenty-nine species of fishes were collected in the middle and upper Colorado River basins in 1967–1973. The native suckers, *Catostomus latipinnis* and *C. discobolus*, were the dominant species in the study area. Introduced species outnumbered native species 19 to 10. The introduced *Ictalurus punctatus* and *Notropis lutrensis* were abundant throughout most of the upper basin. The abundance of introduced species has increased steadily since 1900 as has the introductions of new species. Four endemic species, *Ptychocheilus lucius*, *Gila elegans*, *Gila cypha*, and *Xyrauchen texanus*, are considered endangered. These rare forms reproduce in the lower Yampa River, Desolation Canyon of middle Green River, and the lower Green River in Canyonlands National Park. The major reasons for the decline of native fishes are considered to be alterations of habitat by high dams and introductions of exotic species.

The native fishes of the Colorado River basin comprise a unique fish fauna in North America. Miller (1959) determined that 74% of native Colorado River basin fishes are endemic. This high degree of endemism is integrally tied to the geologic history of the basin, which involved long periods of isolation. The Colorado River begins as a cold, clear stream in the Rocky Mountains, then plunges into a dry desert where it has cut spectacular canyons. In its pristine state it was a warm, turbid, often violent river, given to sudden and drastic changes in volume and turbidity. Endemic fishes of this area can be placed in two categories: small-stream forms found primarily in the lower basin, and large-river forms found in the main stream and larger tributaries throughout the basin. Much of the Colorado system today is composed of large reservoirs with cold, clear tail waters. This, along with water diversion, has had a pronounced effect on the native fish fauna. Miller (1961) and Minckley and Deacon (1968) documented the decrease in native fishes in the lower basin. The large-river fishes are extremely rare, if not extinct, in the lower basin below Lake Mohave (Minckley 1973). Therefore, the upper and middle basins provide the last extensive natural stronghold for these endemic fishes. This group includes *Ptychocheilus lucius* (Colorado squawfish), *Gila cypha* (humpback chub), *Gila elegans* (bonytail chub), *Gila robusta* (roundtail chub), *Catostomus latipinnis* (flannelmouth sucker), and *Xyrauchen texanus* (humpback sucker).

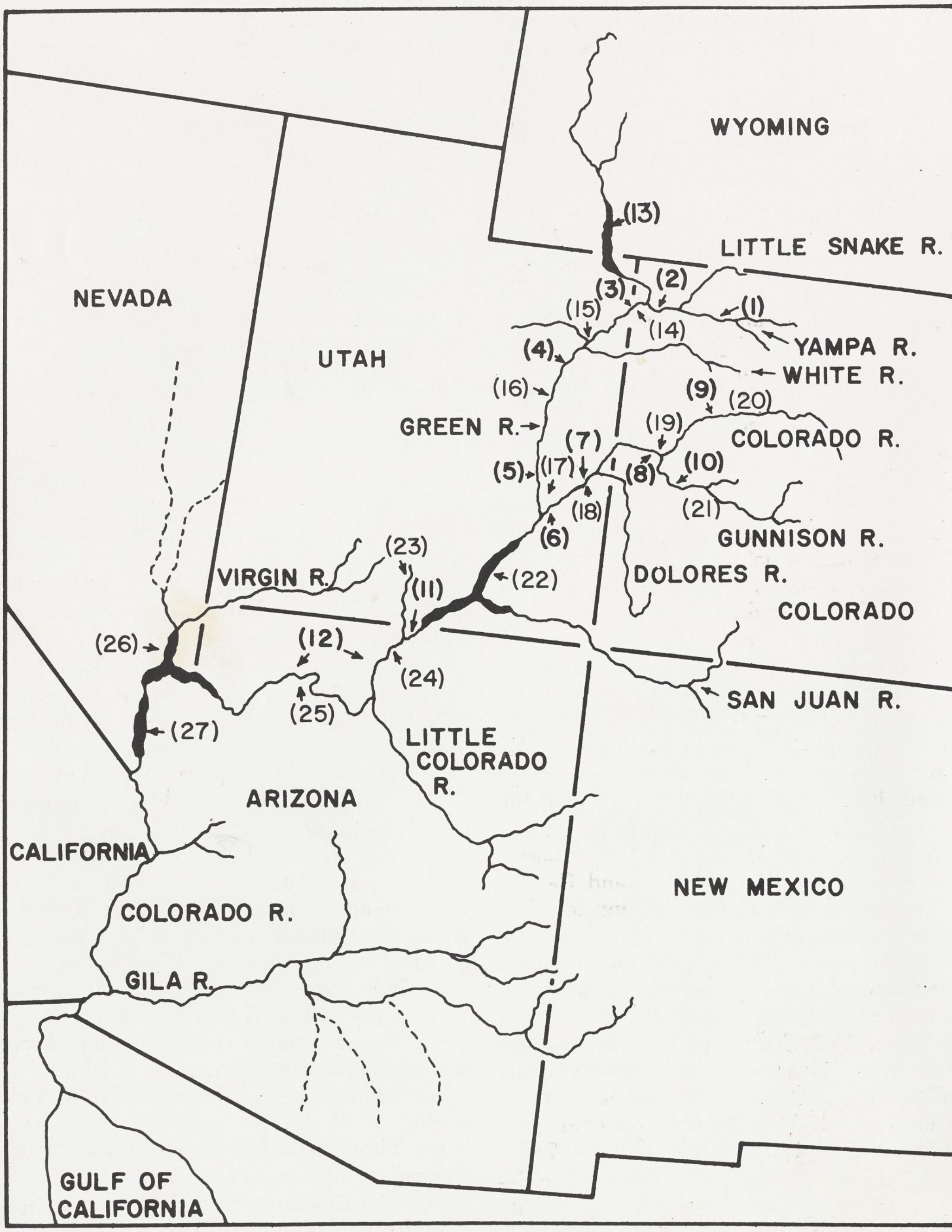

FIGURE 1.—The Colorado River basin showing study areas and other locations mentioned in text. (1)-(12) study areas; (13) Flaming Gorge Reservoir; (14) Dinosaur National Monument; (15) Ouray, Utah; (16) Green River, Utah; (17) Canyonlands National Park; (18) Moab, Utah; (19) Grand Junction, Colorado; (20) Rifle, Colorado; (21) Delta, Colorado; (22) Lake Powell; (23) Paria River; (24) Marble Canyon; (25) Grand Canyon; (26) Lake Mead; (27) Lake Mohave.

Many of the streams in the upper basin flow free, but two major reservoirs were built in the 1960's: Flaming Gorge Reservoir located on the upper Green River and Lake Powell just upriver from Marble and Grand Canyons (Fig. 1).

Evermann and Rutter (1895) summarized collections from the Colorado River made prior to 1894. Taba, Murphy, and Frost (1965) made collections in the Colorado River for several miles below Moab, Utah, and Smith (1959) and McDonald and Dotson (1960) conducted preimpoundment surveys in Glen Canyon. A fish eradication program in September 1962 (Binns et al. 1964) effectively eliminated most native species above and for many kilometers below Flaming Gorge Dam before closure in November 1962. Vanicek, Kramer, and Franklin (1970) documented the distribution of native fishes below this dam following closure, and summarized preimpoundment surveys. They found no reproduction of native fishes in the cold tail waters of the reservoir for 104 kilometers downstream. At that point, the Yampa River joins the Green and ameliorates the coldness of the Green somewhat. Areas not previously studied include the lower 400 km of the Green River, the Yampa River, and the Colorado River above Moab, Utah.

Minckley and Deacon (1968) reported two squawfish taken in the Grand Canyon in the mid 1960's. No subsequent accounts of squawfish from this canyon have been published. Minckley (1973) reported the humpback sucker as nearing extinction below Lake Mohave.

Presently, Colorado squawfish and humpback chub are considered "Endangered" by the U.S. Department of the Interior (1973). Humpback sucker and bonytail chub are also rare (Miller 1972).

The present study was undertaken to determine the status of fishes in the middle and upper Colorado River basins, with special emphasis on endemic, large-river forms.

The objectives were: (1) to determine distribution and relative abundance of fishes in the Colorado River basin above Lake Mead, and (2) to identify areas important for reproduction of endangered forms.

STUDY AREA

That part of the Colorado River basin (Fig. 1) considered in this study includes the Green River system from Craig, Colorado; the Yampa River to the junction of the Green and Colorado Rivers; and the Colorado River from Rifle, Colorado to Lake Mead, excluding Lake Powell. Several larger tributaries also included were the Gunnison River below Delta, Colorado, and the Dolores, Price, White, and Little Snake Rivers.

The main system was divided into 12 sampling areas:

1. The Upper Yampa River from Craig, Colorado, to Juniper Springs, Colorado, approximately 80 km.
2. The Lower Yampa River in Yampa Canyon, Dinosaur National Monument, approximately 72 km.
3. The Green River from the mouth of the Yampa River to the south boundary of Dinosaur National Monument, about 32 km.
4. The Green River from Ouray to Green River, Utah, including Desolation and Grey Canyons, about 192 km.
5. The Green River from Mineral Bottom to its mouth, most of which is in Canyonlands National Park, about 104 km.
6. The Colorado River for 16 km upstream from mouth of the Green River.
7. The Colorado River upstream from Moab, Utah, approximately 32 km.
8. The Colorado River from Grand Junction to Fruita, Colorado, about 16 km.
9. The Colorado River near Rifle, Colorado.
10. The Gunnison River below Delta, Colorado, to its mouth.
11. The Colorado River in Glen Canyon, immediately below Glen Canyon Dam.
12. The Colorado River in Marble and Grand Canyons, Arizona.

Most of the study area consists of canyons; however, major differences exist in fish habitat. Areas 5, 6, and the upper part of 4 are characterized by low gradient and sandy bottoms. The remainder of the basin has high gradients and gravelly bottoms interspersed with areas of sand.

MATERIALS AND METHODS

Fish sampling in the upper and middle Colorado basins was conducted from 1967 to 1973. Gill nets, seines, electrofishing, and hook and line were used. Intensive sampling was conducted near Echo Park at the confluence of the Green and Yampa Rivers in 1968–70. The lower Green River was sampled 1968–71, the upper Colorado River primarily in 1971, Glen Canyon just below Glen Canyon Dam in 1967 and 1970, and Marble and Grand Canyons on three float trips, 1970–72. The latter area was the least intensively studied due to the high cost. Also, the large amount of floating algae, the daily 120–150-cm fluctuations of river level, and deep, swift channels made sampling the main channel extremely difficult. Emphasis was placed on seining shallow areas for juvenile fish, indicators of recent reproduction.

Most fish were returned to the river unharmed, although rare forms dead in gill nets, and occasional specimens from throughout the basin were preserved. All preserved fish were placed in the fish collection of the Utah Cooperative Fishery Unit at Utah State University. Nomenclature follows that recommended by Bailey et al. (1970) except for the humpback chub complex (*Gila cypha*). Reasons for listing these fish as a complex and not a species were given by Holden and Stalnaker (1970).

Fish abundance was recorded in relative terms to better express population status. Definitions of terms follow:

Abundant: The species was collected at will with standard equipment and little effort. Several age groups were present indicating stable reproducing populations. Juveniles were readily taken in one or more habitats by seine.

Common: The species, especially juveniles, was readily collected. Usually more than one age group was represented, suggesting reproduction in the area.

Rare: The species was collected occasionally but with no certainty regardless of effort expended.

Occasional: Occurrence of the species was due to stocking or movement into the area during a particular season, such as winter. The species was usually found in low numbers.

Failure to collect a species in an area did not necessarily mean it was absent but suggested it was very rare.

SPECIES ACCOUNTS

Table 1 summarizes the distributions and abundances determined by this survey.

Salmonidae

Rainbow trout—Salmo gairdneri *Richardson.* Rainbow trout were collected in areas 1, 2, 3, 9, 11, and 12. Their presence was due to planting by government agencies. Rainbow were also found in Rock Creek, a tributary to the Green River, in Desolation Canyon, in 1967, 1968, and 1973. The source of these fish is unknown; flash floods and angling pressure greatly reduced this population during 1969–72. Tapeats Creek in Grand Canyon supported a self-sustaining rainbow trout population fished by hikers and boaters.

An interesting seasonal variation occurred in areas 2 and 3. Rainbow were collected in the cold (10–15 C) Green River above the mouth of the warm (16–22 C) Yampa River during summer months. In spring and fall, 1970, when the Yampa River was cool, they were caught in areas 2 and 3, apparently moving down the Green, invading favorable habitat. Some may also have moved down from the headwaters of the Yampa or up from Jones Hole Creek, a tributary to the Green.

Brown trout—Salmo trutta *Linnaeus.* Brown trout were collected in areas 1, 2, 3 and 10. Originally introduced, most of the brown trout in the study area were wild. They were more common than rainbow in areas 2 and 3 in summer months, probably due to greater tolerance of higher temperatures and turbidity (Embody 1922).

Cutthroat trout—Salmo clarki *Rich-*

TABLE 1.—*Distribution and abundance of fishes in the mainstream of the Colorado River basin above Lake Mead, 1967–1971. (A = Abundant, C = Common, R = Rare, O = Occasional, * = Native)*

	Locality[a]											
	1	2	3	4	5	6	7	8	9	10	11	12
Salmonidae												
Salmo gairdneri	O	O	O	—	—	—	—	—	O	—	A	C
Salmo trutta	O	O	O	—	—	—	—	—	—	O	—	—
Salmo clarki	—	O	O	—	—	—	—	—	—	—	—	—
*Prosopium williamsoni**	A	O	O	—	—	—	—	—	C	—	—	—
Cyprinidae												
Gila atraria	—	—	—	R	—	R	—	—	—	—	—	—
*Gila robusta**	A	A	A	—	—	—	C	A	A	A	—	—
*Gila elegans**	—	R	R	R	R	—	—	—	—	—	—	—
Gila cypha complex*	—	R	R	R	—	—	—	—	—	—	R	—
*Ptychocheilus lucius**	R	R	R	R	R	R	R	R	—	R	—	—
*Rhinichthys osculus**	C	A	A	R	R	—	C	A	C	A	—	A
Richardsonius balteatus	C	A	A	—	—	—	—	—	—	—	—	—
Pimephales promelas	C	C	C	C	C	C	C	C	C	C	—	R
Cyprinus carpio	C	C	C	C	C	C	C	A	—	C	C	C
Notropis lutrensis	—	R	R	A	A	A	A	A	—	A	—	—
Notropis stramineus	—	—	—	—	—	—	A	A	—	—	—	—
Semotilus atromaculatus	—	C	C	—	—	—	—	—	—	—	—	—
Catostomidae												
*Catostomus latipinnis**	C	A	A	A	A	A	A	A	A	A	A	C
*Catostomus discobolus**	A	A	A	C	R	R	C	A	A	A	—	C
Catostomus commersoni	A	R	R	—	—	—	—	—	R	—	—	—
Catostomus catostomus	—	—	—	—	—	—	—	—	R	—	—	—
*Xyrauchen texanus**	—	R	R	R	R	R	—	R	—	—	—	—
Ictaluridae												
Ictalurus punctatus	R	A	A	A	A	A	A	C	—	R	C	R
Ictalurus melas	—	R	R	R	C	—	R	—	—	—	—	—
Cyprinodontidae												
Fundulus zebrinus	—	—	—	—	—	—	R	R	—	R	—	—
Centrarchidae												
Micropterus salmoides	—	O	—	O	—	C	R	R	—	—	—	—
Lepomis macrochirus	—	O	—	—	—	—	—	—	—	—	—	—
Lepomis cyanellus	—	R	R	R	R	R	C	C	—	C	—	—
Percidae												
Stizostedion vitreum	—	O	—	O	—	—	—	—	—	—	—	—
Cottidae												
*Cottus bairdi**	—	R	R	—	—	—	—	—	—	—	—	—
Hybrids												
Catostomus latipinnis × *Xyrauchen texanus*	—	R	R	R	R	R	R	R	—	—	—	—
Catostomus discobolus × *Catostomus commersoni*	A	R	—	—	—	—	—	—	—	—	—	—
Catostomus latipinnis × *Catostomus commersoni*	R-C	R	—	—	—	—	—	—	—	R	—	—

[a] 1 Upper Yampa; 2 Lower Yampa; 3 Green (DNM); 4 Desolation Canyon; 5 Green (CNP); 6 Colorado (CNP); 7 Colorado-Moab; 8 Colorado-Grand Junction; 9 Colorado-Rifle; 10 Lower Gunnison; 11 Glen Canyon; 12 Marble and Grand Canyon

ardson. Cutthroat trout were collected in areas 2 and 3. Only eight were taken during the study (Table 2). These fish are considered wanderers from nearby cold water areas where they were stocked.

Mountain whitefish—Prosopium williamsoni *Girard.* Mountain whitefish were abundant in area 1 and common in area 9. Single specimens were caught in areas 2 and 3, apparently wanderers from area 1. Juveniles were found in areas 1 and 9.

Cyprinidae

Utah chub—Gila atraria *Girard.* Only two Utah chubs were collected during the present study, one in area 4, the other in area 6. They have been reported from the upper Colorado basin by Smith (1959),

TABLE 2.—*Number of adult fish taken in the Colorado River system above Lake Mead 1967–1973 primarily with gill nets and electrofishing gear*

Species	1967	1968	1969	1970	1971	Total
Salmonidae						
Salmo gairdneri		3	7	24	many	>34
Salmo trutta		0	15	7	2	24
Salmo clarki		2	0	6	0	8
Prosopium williamsoni		1	0	1	many	>2
Cyprinidae						
Gila robusta		180	105	60	30	375
Gila elegans		29	3	4	0	36
Gila cypha complex	22	6	26	6	1	61
Ptychocheilus lucius		71	90	127	12	300
Catostomidae						
Catostomus latipinnis		1983	1709	2400	many	>6092
Catostomus discobolus		479	276	318	many	>1073
Catostomus commersoni		5	6	39	many	>50
Xyrauchen texanus		6	4	33	10	53
Centrarchidae						
Micropterus salmoides		0	0	1	0	1
Lepomis macrochirus		0	1	0	0	1
Lepomis cyanellus		1	1	0	5	7
Percidae						
Stizostedion vitreum		0	4	4	0	8
Hybrids						
Catostomus latipinnis × *Xyrauchen texanus*		5	6	27	2	40
Catostomus discobolus × *Catostomus commersoni*		4	1	3	many	>8
Catostomus latipinnis × *Catostomus commersoni*		0	1	9	several	>10

McDonald and Dotson (1960) and Sigler and Miller (1963). The original introduction was probably as released baitfish. This species, so often a pest fish, apparently has not found suitable conditions in the study area. They are flourishing in Flaming Gorge Reservoir.

Roundtail chub—Gila robusta *Baird and Girard.* Historically, the roundtail chub has been the dominant native carnivore of tributaries in the Colorado basin. It is abundant in areas 1, 2, 3, 9, and 10, but diminishes rather rapidly downstream from these areas in both the Green and Colorado Rivers. This general type of distribution was noted by Jordan and Evermann (1896) as they reported roundtail to the "base of the mountains" in the Gunnison River. The round tail was also abundant in major tributaries such as Little Snake, Duchesne, White, Price, and Dolores. It was collected from all habitats, riffles to stagnant backwaters. Little change in historic distribution and abundance was noted.

Bonytail chub—Gila elegans *Baird and Girard.* The endemic bonytail chub is very rare in the Colorado basin. It was collected in areas 2, 3, 4, and 5; only 36 were taken. Historically, it was found in the main channels of rivers below the range of the roundtail chub (Jordan and Evermann 1896). Vanicek and Kramer (1969) calculated strong year classes of bonytail chub for 1959, 1960, and 1961 in area 3 from adults collected in 1964–66. A search through samples of several hundred young chubs collected in area 3 by Vanicek and Kramer and during the present study revealed only three possible bonytail chubs. This scarcity suggests that for the last several years bonytail chubs have not reproduced well where they were once successful. Also, the concomitant decrease in adult numbers suggests this species is rapidly losing ground in an area where it was recently abundant. The period of decrease corresponds to the time Flaming Gorge Dam has been closed.

Bonytail chubs were apparently once

abundant throughout their range. Older fishermen remembered catching them readily as youths. Jordan (1891) seined several from the Gunnison River near Delta and at Green River, Utah. Thus, once a common fish, it is now very rare.

Humpback chub complex—Gila cypha *Miller*. Members of the humpback chub complex were collected in areas 2, 3, 4, and 11. Most specimens were taken from eddies adjacent to fast currents. Only 61 were taken. Of these, 26 were collected near Echo Park in areas 2 and 3 in 1969, most from one eddy. Fifteen were taken in area 11 in 1967; only one was taken in the same area with increased effort in 1970, suggesting a decrease in abundance had occurred. Young chubs collected in area 4 had noticeable nuchal humps and other characters suggesting they were of the humpback chub complex. Juveniles were not found in any other area.

The humpback chub was first described by Miller (1946) and has been seldom collected since that time. Smith (1960) reported 18 from Hideout Canyon of the Flaming Gorge basin, most from one small area. Sigler and Miller (1963) reported it from the Colorado River near Moab, Utah, and the White River near Bonanza, Utah. Utah and Arizona Fish and Game personnel collected numerous members of this complex in Lake Powell in the early-mid 1960's (Holden and Stalnaker 1970). Few specimens have been seen there recently (Steve Gloss, Utah Division of Wildlife Resources, personal communication). Miller (1955) reported remains of this group from archaeological sites in the lower Colorado basin. Thus, this form ranged throughout the main stream of the Colorado basin, and it appears doubtful that it was abundant in the 20th Century as few published accounts are available.

Colorado squawfish—Ptychocheilus lucius *Girard*. Colorado squawfish were collected throughout the study area in small numbers. Three hundred adults were collected, 261 of these from area 2. Young-of-the-year squawfish were collected in area 4 in 1971 and 1972 and in area 5 in 1970 and 1971. Juveniles were abundant around Echo Park in 1968, but very few were caught in 1969 and none could be located in 1970 or 1971, undoubtedly a reflection of poor spawning success. Reasons for this are unknown as the numbers of adults did not decrease. Vanicek and Kramer (1969) found that successful spawning was the rule, with very few weak year classes of squawfish in this area.

Juveniles were collected in small numbers in areas 4 and 5 throughout the study. Three juveniles were collected in area 7 in 1971.

Adults were collected in all habitat types but mainly in slow water (eddies, backwaters, and flooded canyon mouths). Juveniles were caught in backwater areas and small eddies typically 60–90 cm deep. Young of the year were taken in shallow, warm, stagnant areas usually between a sandbar and the bank.

Congregations of ripe male squawfish were collected in area 2 in July and early August of each year, 1968–70. The origins of this migration are not known, although reproduction is the hypothesized purpose (Holden and Stalnaker 1974). One or two squawfish were taken by fishermen each year in Lake Powell, but no large numbers have been noted (Steve Gloss, Utah Division of Wildlife Resources, personal communication).

Colorado squawfish have been reported to reach at least 36 kg and 150 cm in length (Jordan and Evermann 1896). The largest specimens seen during the study were not weighed but were estimated at 7 kg. Older fishermen recall catching a fair number of fish near 22 kg, and stories of larger fish were common till the 1930's. Several reasons for the decline were cited by fisherman, the most common being construction of dams. This fish has apparently suffered great reductions in population size within the last 30 to 40 years.

Speckled dace—Rhinichthys osculus *Girard*. The native speckled dace was collected throughout the study area. It was abundant in most areas, but less common in large, warm sections of the main rivers.

In areas 3 and 8, they often comprised the majority of specimens in seine hauls. Dace were collected in most habitats, but were typically associated with small riffles or areas of current. In area 12 they were abundant in almost all tributaries, but were not collected in the main river except at mouths of tributaries. Several specimens collected in area 5 in 1970 appeared extremely silvery and lacked spots or blotches. Later attempts in the same area failed to produce additional specimens. The silvery color was assumed to be a response to the turbid water and sandy bottom of the area. This phenomenon is common among fishes inhabiting such areas (flannelmouth suckers in the same area were also silvery).

Redside shiner—Richardsonius balteatus *Richardson.* The introduced redside shiner was abundant in areas 1, 2, and 3. The redside shiner was collected by seine from most habitats except fast water and riffles. Simon (1946) reported that this fish was established in upper Green River of Utah and Wyoming in 1938. A decrease in redside shiner abundance was noted near the southern boundary of Dinosaur National Monument in 1971 when red shiners became common there.

Fathead minnow—Pimephales promelas *Rafinesque.* Fathead minnows were common throughout much of the study area but never abundant. Only one was taken in area 12. They were seldom taken in areas of current but typically were found in quiet backwaters. They may have become common in various parts of the basin at different times due to introduction as baitfish. Miller (1952) reported the use of fathead minnows as baitfish on the lower Colorado River, but suggested they were not then common in the river. Miller and Lowe (1964) reported fatheads in the Paria River at the lower end of Glen Canyon, in 1952. Smith (1959) made the first Utah collection in Glen Canyon, and Smith (1960) first reported fatheads from upper Green River of Utah. No earlier reports of fatheads in the Colorado basin exist; therefore the site and date of introduction is unknown. Due to small populations the fathead minnow is not now a serious competitor of native species.

Carp—Cyprinus carpio *Linnaeus.* The ubiquitous carp was taken throughout the study area, but seldom in large numbers. It was abundant only in area 8 and a few quiet water areas throughout the study area. The area near Grand Junction (area 8), although of rapid current, was enriched by man's activities, providing excellent carp habitat. The area below the city sewage disposal plant was extremely productive of carp; many were very large.

Small carp were seined from most slow backwaters throughout the study area, although seldom in large numbers. Adult carp were often seen feeding on surface debris in eddies. Beckman (1952) reported that carp were introduced into Colorado in 1882. It may have moved into the Colorado River system soon thereafter.

Red shiner—Notropis lutrensis *Baird and Girard.* A newcomer to the upper Colorado River basin, the red shiner was extending its range up the Green River during the study. This species was abundant in the Colorado River and the Green River upstream to Desolation Canyon in 1968. A few specimens were collected at Ouray, Utah, in 1969. It was common to abundant in the Green River near the southern boundary of Dinosaur National Monument by 1971. Two specimens were collected near Echo Park and one in the White River in 1971 also.

Red shiners were collected from most habitats, except fast water, and were the most abundant fish in seine hauls from the middle Colorado and lower Green Rivers.

Miller (1952) doubted the red shiner, then being used as a baitfish, would become established in the lower Colorado basin due to unfavorable habitat. However, Hubbs (1954) reported the shiner established in that same area by 1953.

The question arises whether this species entered the upper basin through Grand Canyon, or whether it was separately introduced. Neither Smith (1959) nor McDonald and Dotson (1960) collected the red shiner in Glen Canyon. Judging from present data, Glen Canyon should have been ideal habitat for this species. Taba, Murphy, and Frost (1965) reported that the red shiner was very abundant near Moab, Utah, in 1962–63. Stone, Fields, and Miller (1965) reported that the red shiner "exploded" in 1963 in Lake Powell. It is therefore doubtful whether this fish, not present in Glen Canyon in 1959, could become so abundant over 200 miles upstream by 1962, if it moved upriver from the lower Colorado basin. More probable is an introduction near Grand Junction, Colorado, in the late 1950's or early 1960's, with subsequent downstream movement and more recent movement up the Green River.

Sand shiner—Notropis stramineus *Cope*. The sand shiner was first reported from the upper Colorado basin by Holden and Stalnaker (1974). It was collected in 1971 in areas 7 and 8, also in the Dolores River. It was abundant and may spread much as the red shiner. Its numbers and distribution suggest it had been present for several years, perhaps introduced as a baitfish, as it is common in the South Platte River system of eastern Colorado.

The sand shiner was inadvertently planted into the Little Colorado River in 1938 (Miller and Lowe 1964).

Creek chub—Semotilus atromaculatus *Mitchill*. Another introduced cyprinid is the creek chub. It was found only around Echo Park in areas 2 and 3. Vanicek, Kramer, and Franklin (1970) found it below Flaming Gorge Dam, collecting only 12 specimens in four years. Most of these were taken in the area between the Dam and the mouth of the Yampa River. Simon (1946) reported the creek chub's presence in the Little Snake River. Therefore, it has been in the Green River system for some time but apparently has not found conditions favorable for maintaining large populations.

Catostomidae

Flannelmouth sucker—Catostomus latipinnis *Baird and Girard*. The flannelmouth sucker is by far the most abundant large native species. Well over 6000 adults were collected during the study (Table 2). Adults and young were caught in all study sections. The species was least abundant in areas 5 and 6. They were collected in all habitat types, fast current, riffles, eddies, and stagnant backwaters. In area 12 they were collected only in tributary streams.

In upper parts of the study area, flannelmouth suckers were usually dark brownish-green dorsally, yellowish or orange laterally, and white ventrally. In river sections of generally more turbid water and sand bottom, they were light tan on the back and silvery white on the sides and belly.

Bluehead sucker—Catostomus discobolus *Cope*. The bluehead sucker is abundant in areas 1, 2, 3, 8, 9, and 10; common in 4, 7, and 12; and rare in 5 and 6. This distribution corresponds to the relative amount of rocky substrate in the various areas. The bluehead sucker was usually collected over rocky bottom and was common in riffles. In the sandy bottom reaches of the study area it was collected only over the few rocky areas created by talus slopes extending into the river. Bluehead suckers were also common in clear, rocky tributary streams. Stream specimens seldom exceed 20 cm in total length, whereas 25–30 cm specimens are common in the main river. In area 12 they were collected only in tributaries, but were common in riffle habitats of the main stream in 1968 (J. E. Deacon, personal communication).

The bluehead sucker is polymorphic in the Colorado River system with slender and deep peduncled forms present. The slender peduncled type is thought to be adapted for swift-water areas (Miller 1946). Both forms were collected during the study, as were intermediate individuals. All types were collected together. Deep forms are most common in the upper, colder parts of the basin and slender forms most common in the middle sections, especially area 4. No difference in habitat preference was noted when they were collected together.

Little or no difference was noted in the historical distribution or abundance of this species (Jordan and Evermann 1896).

White sucker—Catostomus commersoni *Lacépède*. The introduced white sucker is abundant only in area 1. It was rare in area 2 in 1968 and 1969 but was collected there in greater numbers in 1970 (Table 2). It is also rare in areas 3 and 9. The white sucker is very common in areas upstream from the study area, at times becoming a nuisance in areas managed for trout.

Hubbs, Hubbs, and Johnson (1943) stated the white sucker was introduced into the Colorado River in about 1926; Miller (1952) said it was introduced in the Colorado above Rifle about 1938. Separate introduction into upper Yampa River is assumed from its present distribution.

Longnose sucker—Catostomus catostomus *Forster*. The longnose sucker is another introduced sucker very common in the headwaters of the upper Colorado basin. Only one longnose sucker was collected during the study in area 9. A species associated with colder trout habitat, it apparently invaded the study area occasionally. Beckman (1952) stated that the longnose sucker has "just recently" been planted in the Colorado system.

Humpback sucker—Xyrauchen texanus *Abbott*. The endemic humpback sucker was collected only in the middle and lower sections of the study area. It is rare in all areas; only 53 were taken during the study. It was collected almost exclusively in stagnant or quiet-water areas. Humpback suckers were caught in relatively large numbers (10–15) in a quiet, cutoff channel at the mouth of Yampa River in early March and late November, 1970. They were also concentrated in flooded mouths of washes in Canyonlands National Park area during high water of early summer, 1971.

Juvenile humpback suckers are relatively unknown. Winn and Miller (1954) described larval humpback suckers collected below Lake Mead. Douglas (1952) reported spawning humpback suckers from Lake Havasu, and Jonez and Sumner (1954) observed spawning in Lakes Mead and Mohave, but no juveniles were reported later (Minckley and Deacon 1968). Smith (1959) collected two specimens 3.75 cm in length from Glen Canyon. It is probable that young humpback suckers appear nearly identical to young flannelmouth suckers on field examination and are not easily distinguished.

Jordan (1891) found the humpback sucker abundant in the study area, where local residents used it a great deal for food. Its large size (3.6–4 kg) and easy accessibility with seines made it an ideal food fish. Vanicek, Kramer, and Franklin (1970) reported that humpback suckers were relatively rare in area 3 but suggested they were also rare before closure of Flaming Gorge Dam.

The data indicate a marked reduction in humpback suckers during this century, from abundance to extreme rarity.

Ictaluridae

Channel catfish—Ictalurus punctatus *Rafinesque*. One of the most common fishes of the middle and upper Colorado basin, the introduced channel catfish, has readily adapted to favorable habitat. Channel catfish are abundant in the middle sections of the study area, becoming rare in the upper, cooler sections and below Lake Powell (Table 1). Adults were seldom taken with conventional collecting gear but were readily caught on hook and line. They were very evident surface feeders. During a large mayfly hatch in Desolation Canyon August 9, 1968, the surface of the river was teeming with feeding channel catfish. The average total length was estimated to be 15–20 cm.

Age 0 and I catfish were collected by seine in areas of gentle current and backwaters. Adults appear to be most common in eddies but were taken in all habitats. The largest specimen collected during the study was 5.9 kg. Fishermen reported much larger individuals. This species supports a small fishery in accessible parts of the study area.

Jordan (1891) suggested stocking channel catfish in the Colorado River. Miller and Alcorn (1943) reported that the earliest introductions in the lower basin were in

1892–93 or 1906. It apparently became established throughout the Colorado River system in the early 1900's, as many older fishermen believed it to be a native species.

Black bullhead—Ictalurus melas *Rafinesque*. The black bullhead is rare in the upper and lower sections of the study area, but more abundant in the slower water of Canyonlands National Park. It was collected exclusively in stagnant water areas, and usually only one or two individuals were taken in any one sample.

Ellis (1914) reported that the species was successfully raised in ponds near Montrose and Grand Junction, Colorado. Thus, an early introduction into the river was possible.

Cyprinodontidae

Rio Grande killifish—Fundulus zebrinus *Jordan and Gilbert*. The introduced Rio Grande killifish was collected only from the Colorado River and its tributary, the Gunnison River. It was not common; seldom were more than one or two taken in an area. The killifish was reported in Glen Canyon in 1954 and 1958 by Smith (1959) and in 1959 by McDonald and Dotson (1960). Miller and Lowe (1964) reported that this species was inadvertently introduced into Little Colorado River in 1938. It may have spread upstream from this point but more likely was introduced separately into the upper basin as a baitfish.

Centrarchidae

Largemouth bass—Micropterus salmoides *Lacépède*. The introduced largemouth bass is common only in area 6. Most of these fish are assumed upstream migrants from Lake Powell. The largemouth is rare in the remainder of the Colorado River to Grand Junction. Juvenile bass, age group I, were most commonly found. Spawning may occur in ponded areas along the river in area 8 and perhaps also area 6.

One adult bass was collected in area 2 in 1970, one in area 4 in 1971, and one in area 11 in 1970.

Largemouth bass were present in Glen Canyon in 1958 (McDonald and Dotson 1960), being originally stocked in Lake Mead in 1939 (Miller and Alcorn 1943).

Bluegill—Lepomis macrochirus *Rafinesque*. One adult bluegill was collected in area 2 in 1969. It may have originated from a pond either in upper Yampa drainage or Duchesne River system. Bluegill are in Lake Powell but were not collected in the Canyonlands National Park area.

Green sunfish—Lepomis cyanellus *Rafinesque*. Green sunfish were collected throughout the study area except in areas 1, 9, 11, and 12. They were almost exclusively taken in quiet, backwater areas. In the Green River system they are rare. Hundreds of young of the year were found in a small, drying cutoff pool in Desolation Canyon in 1969. Green sunfish are common in Colorado River. Apparently the slower water of the Colorado offers better habitat for this species than the Green River.

Green sunfish were collected in the lower Colorado basin in 1926 (Miller and Lowe 1964). Wallis (1951) suggested that this species was inadvertently planted in Lake Mead in 1937. McDonald and Dotson (1960) reported green sunfish to be abundant in Glen Canyon. R. R. Miller (personal communication) collected it in area 12 in 1968. It is not known whether this species moved up the Colorado River to the upper basin or was separately introduced.

Percidae

Walleye—Stizostedion vitreum *Mitchill*. Walleyes were taken occasionally in area 2, one in 1969 and four in 1970. They are somewhat more common at Ouray; three were collected in one week in March, 1969. The suspected source of these fish is the Duchesne River system, where walleye were stocked in a small reservoir.

Cottidae

Mottled sculpin—Cottus bairdi *Girard*. Mottled sculpin were collected only at Echo Park. Being a cool water species, it is common in the upper, cold water parts of the basin (Beckman 1952).

Hybrids

Flannelmouth sucker × humpback sucker hybrid. Hybrids between the flannelmouth and humpback suckers were collected throughout the range of the humpback sucker, usually in quiet, backwater areas in association with humpback suckers. They were readily distinguished by an intermediate lateral line scale number and a much abbreviated, although distinct, keel behind the occiput. This hybrid was rare, 40 being collected during the study, but was nearly as numerous as the humpback suckers collected during the study.

Hubbs and Miller (1953) described this hybrid from eight specimens, two from the upper Colorado River system and six from the upper Green River. Jordan (1891) collected one of the above specimens in 1889 from the Delta, Colorado, area. Banks (1964) reported this hybrid from area 3 before closure of Flaming Gorge Dam. Vanicek, Kramer, and Franklin (1970) collected 16 hybrids from the same area after closure of the dam. No fertile hybrids have been reported even though hybrids have been known for over 75 years.

Bluehead sucker × white sucker hybrid. The hybrid between the bluehead and white suckers was found only in the Yampa River. It is extremely abundant in area 1 and rare in area 2, as is the white sucker. Hubbs, Hubbs, and Johnson (1943) described this hybrid from the upper Colorado and Gunnison Rivers. Baxter and Simon (1970) reported it from a tributary of the Little Snake River in Wyoming. It appears to be distributed in the upper parts of the basin following the range of the white sucker.

Flannelmouth sucker × white sucker hybrid. The flannelmouth × white sucker hybrid is rare to common in area 1, rare in 2, and rare (one specimen) in 10. It was collected in 1969, 1970, and 1971. Baxter and Simon (1970) reported this hybrid from Big Savery Creek, tributary of the Little Snake River, Wyoming, but no description has been published.

DISCUSSION

Twenty-nine species were collected during the study, of which 19 were introduced. All native species previously reported from the study area were collected except one. Taba, Murphy, and Forst (1965) reported the mountain sucker *(Catostomus platyrhynchus)* from the Colorado River below Moab. They distinguished it from the bluehead sucker by the presence of notches at the side of the mouth. Smith (1966) reported side notches as a characteristic of the subgenus *Pantosteus*, and that they were well developed on both the bluehead and mountain suckers. Also, the mountain sucker is characteristically found in small, cold mountain streams. Therefore, the above report is probably a case of mistaken identification.

The diversity of species is greater in the more heterogeneous high gradient, rocky bottom habitats than low gradient, sandy bottom areas. For example, high gradient areas 2 and 3 (Table 1) had 28 and 23 species present, respectively, whereas low gradient areas 5 and 6 had only 13 and 12. Total fish numbers are also considerably higher in rocky areas.

Areas 7 and 8 are exceptions to this generalization. Each of these high gradient areas support only 15 species, compared with 25 from similar areas in the Green River basin. Total fish numbers are similar in both areas, although native species dominated the Green and introduced species the Colorado River. This was pronounced among juvenile fishes. Areas 11 and 12 were sampled less intensely than other sections of the study area, which might account for the low diversity found there. Red shiners and green sunfish are also known from area 12 (R. R. Miller, personal communication).

Flannelmouth and bluehead suckers are the dominant fish in the study area. Colorado squawfish, bonytail chub, humpback chub, and humpback sucker are very rare and undoubtedly are threatened with extinction if man continues to alter their habitat. The Yampa River, particularly the lower portion, and the middle and lower

Green River—areas 4 and 5—now harbor these forms. Reproduction of the rare fishes was evident only in these areas. Therefore, any alteration of the Green River system below Flaming Gorge Dam will undoubtedly be harmful to these rare fishes, acutely so in the Yampa River and Desolation Canyon.

The reasons for the decline in native fish abundance are numerous. The most obvious factor is high dams with their resultant reservoirs and cold tail waters. Neither reservoirs nor tail waters provide suitable habitat for the reproduction of endemic species. Dams have been described as the major decimating factor for fish in the lower Colorado basin (Minckley and Deacon 1968) and the 104 km below Flaming Gorge Dam (Vanicek, Kramer, and Franklin 1970). The present study indicates the Colorado River of Glen, Marble, and Grand Canyons should be added to this list.

Lowered temperatures of the Colorado River in Glen, Marble, and Grand Canyons as a result of cold discharge from Glen Canyon Dam, and in conjunction with little solar warming because of high canyon walls and no large, warm tributaries, have made it unfavorable for most native fishes. Spawning temperatures, especially for rare forms, seldom occur. A daily 120–150 cm fluctuation in river level precludes the availability of warm, rich backwaters preferred by juvenile fish in the upper basin. Secondary production appears very limited in the main river; few aquatic insects are seen in, what appears to be, a very sterile environment. It is probable that members of the humpback chub complex collected here were remnants of small populations existing before dam closure. It is likely that other adult "large-river" species exist, but once they are gone no young will be available to repopulate the area. Perhaps the decrease in chubs in area 11 between 1967 and 1970 was indicative of this change. Only those native species adapted to tributary streams (speckled dace, bluehead and flannelmouth suckers) are likely to survive.

Native fish abundances in the Green River of Dinosaur National Monument below the mouth of the Yampa River has changed since 1966. This study has shown a decrease in young Colorado squawfish and adult bonytails chubs from that reported by Vanicek, Kramer, and Franklin (1970). We believe the reason for this is an unnatural decrease in mid-summer river temperature, especially since 1965, due to Flaming Gorge Dam, but this requires further documentation.

Another reason for the decline in endemic fish numbers in the upper basin is competition from introduced species, as has been documented in the lower basin. The Colorado squawfish and humpback sucker have become rare during the first half of the 20th Century. During this same period the channel catfish became well established. The addition of an abundant carnivore to the fish fauna has created additional competition for space and food. More recent introduction of now abundant small cyprinids (specifically the red shiner) have created more competition for space and food with juvenile fish. This hypothesis may partly account for the lower abundance of endemic fishes in the Colorado River as compared with similar areas in the Green River. Most introductions in the upper basin apparently have occurred in the Colorado River, probably from released baitfish.

The future does not look bright for the Colorado River and its endemic fishes. Increased human population and use of Colorado system water will undoubtedly continue to deteriorate the quality of the environment. Only a small portion of the system now retains the requirements for successful populations of indigenous fishes. Little additional alteration may be all that is needed to push these species to extinction. Perhaps it is the Colorado River environment which should be considered "Endangered."

ACKNOWLEDGMENTS

The authors are especially indebted to the late Robert H. Kramer who provided much valuable guidance during this project. Personnel of the Utah Division of Wildlife Resources, Colorado Division of Game, Fish, and Parks, Dinosaur National Monument, Canyonlands National Park, and Grand Canyon National Park were helpful with information and collecting permits. Support for the project came from the Utah Cooperative Fishery Unit, a joint venture of Utah State University, Utah Division of Wildlife Resources, and the U.S. Fish and Wildlife Service, and a National Wildlife Federation Fellowship and NDEA Fellowship to the senior author.

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SPECIES RELATIONSHIPS AMONG FISHES OF THE GENUS *GILA* IN THE UPPER COLORADO RIVER DRAINAGE[1]

Gerald R. Smith[2], Robert Rush Miller[2], and W. Daniel Sable[3]

Taxonomic treatment of the chubs of the *Gila robusta* complex (family Cyprinidae) that inhabit the Colorado River basin and certain rivers in north-western Mexico (Figure 1) is problematical and requires study of the entire group for final resolution. It is intended to do this, but in this paper we present data demonstrating that there are three species of this complex in the Colorado River and its major tributaries, from the Grand Canyon region upstream. These chubs are the most extreme members of the genus in their specialization for life in the unique big-river habitat of the Colorado River.

Our objectives are (1) to determine the validity and relationships of the roundtail, bonytail, and humpback chubs in the big-river habitat; (2) to determine their relationships to other populations of *Gila* in the middle and upper Colorado River basin; and (3) to find characters useful for identifying young and adult *Gila robusta* Baird and Girard, *G. elegans* Baird and Girard, and *G. cypha* Miller, and possible hybrids. We do not at this time treat the complex representatives of *Gila* in the Gila River basin (see Rinne, 1976), except to note that *G. intermedia* (Girard) may be a separate evolutionary line, secondarily related to *G. robusta*.

Misinterpretation of the patterns of variation in the nuchal hump and lack of decisive, objective evidence has been the main cause of disagreement among those studying the *G. robusta* complex. The nuchal convexity has never been measured precisely or quantitatively related to other characters. For example, Holden and Stalnaker (1970) used subjective code values for the form of the nuchal hump, and coded continuous morphometric variables (23.1 15.8, etc.) into discontinuous states ("A", "B", etc.), thus losing much of the resolving power of the measurements. The clustering illustrated by them shows only the level at which specimens join clusters; it does not show intermediacy, and it cannot display the morphological relationship of a specimen between other specimens. Thus there is no way to evaluate the supposed "intergrades" cited by Holden and Stalnaker: in their paper the "intergrades" may appear as a result of the method of coding data. They were unable to determine whether the so-called intergrades were part of one variable complex or two incompletely separated species. In contrast, we find that there are very few intermediates, in the Green River at least, and that most specimens, including the "intergrades" shown by Holden and Stalnaker (1970: Figure 4), can be assigned to one of the two species *cypha* or *elegans*.

Our analysis consists of two parts. First, principal components analysis of 34 meristic and morphometric characters, not including a direct measure of the nuchal hump, is used to establish clear evidence of morphological segregation of the large-river specimens into three distinct clusters. It is important to establish that the segregation is not based on the nuchal hump or other subjective characters, but on a broad range of body proportions, fin-ray counts, and vertebral numbers, presumably with a broad genetic basis. Second, after establishing the existence of three separate populations, with little or no overlap, at least within the unmodified, large-river habitat, individual discriminating key characters are developed for identification of these fishes in the laboratory and field. Such characters are critically needed to end the confusion that has clouded attempts to formulate a sound management policy for these endangered or threatened fishes. The population analysis and the development of key characters were conducted separately by us in order to avoid circular taxonomic logic and to enable the two systems to serve as useful tests of one another.

Principal components analysis, a multivariate statistical method enabling taxonomic use of combined (correlated) information from many characters, was applied to 34 characters of 140 specimens. These characters are: dorsal, anal, pectoral, and pelvic fin-rays (rays from both paired fins recorded); standard length, head length, eye diameter, snout length, preanal length, head depth through eye, head depth at occiput, interorbital width, occiput to tip of snout, dorsal-fin basal length, anal-fin basal length, predorsal length, pectoral-fin length, pelvic-fin length, upper jaw length, mouth width, body depth over pelvic insertion, caudal-peduncle depth, anal origin to caudal base; number of vertebrae; pharyngeal arches, total length, width, length of anterior limb, and length of posterior limb, of both left and right arches (eight characters). This analysis discriminated the populations in question (Figures 2-5) showing the major trends in variation, the characters dominant in the trends, and the characteristics of typical as well as intermediate individuals.

A graph of 140 individuals plotted according to their scores on principal components I and II,

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[1]Completion of this paper was delayed by closure of upper Green River to scientists other than federally funded personnel during the five-year period 1963-1967. Considerable aid was received from a number of organizations and individuals. Included are research grants to R. R. Miller from the Horace H. Rackham School of Graduate Studies (1950), the National Science Foundation (G-15914, 24129, 24465, GB-3271, 4854, 6272X), and the National Park Service (1975), with cooperation from the various western states for collecting permits. Frances H. Miller recorded and calculated data, helped prepare the distribution map, and criticized drafts of the manuscript. Jeffrey N. Taylor prepared the original plots for Figure 1. Loans of specimens were received from the U.S. National Museum (E. A. Lachner, S. H. Weitzman, W. R. Taylor, Susan Karnella), Arizona State University (W. L. Minckley), Bell Museum of Natural History (Samuel Eddy, H. B. Tordoff, C. W. Huver), and the Museum of Northern Arizona (S. E. Carothers). Mark J. Orsen (of the Museum of Zoology) and Karna M. Steelquist (of the Museum of Paleontology) prepared the drawings and other illustrations, except Figure 10, taken by Bruce J. Turner. Abbreviations are: UMMZ (University of Michigan Museum of Zoology) and USNM (U.S. National Museum of Natural History).

[2]Museum of Zoology, University of Michigan, Ann Arbor, MI 48109.

[3]Wisconsin State University, Whitewater, Wisc. 53190.

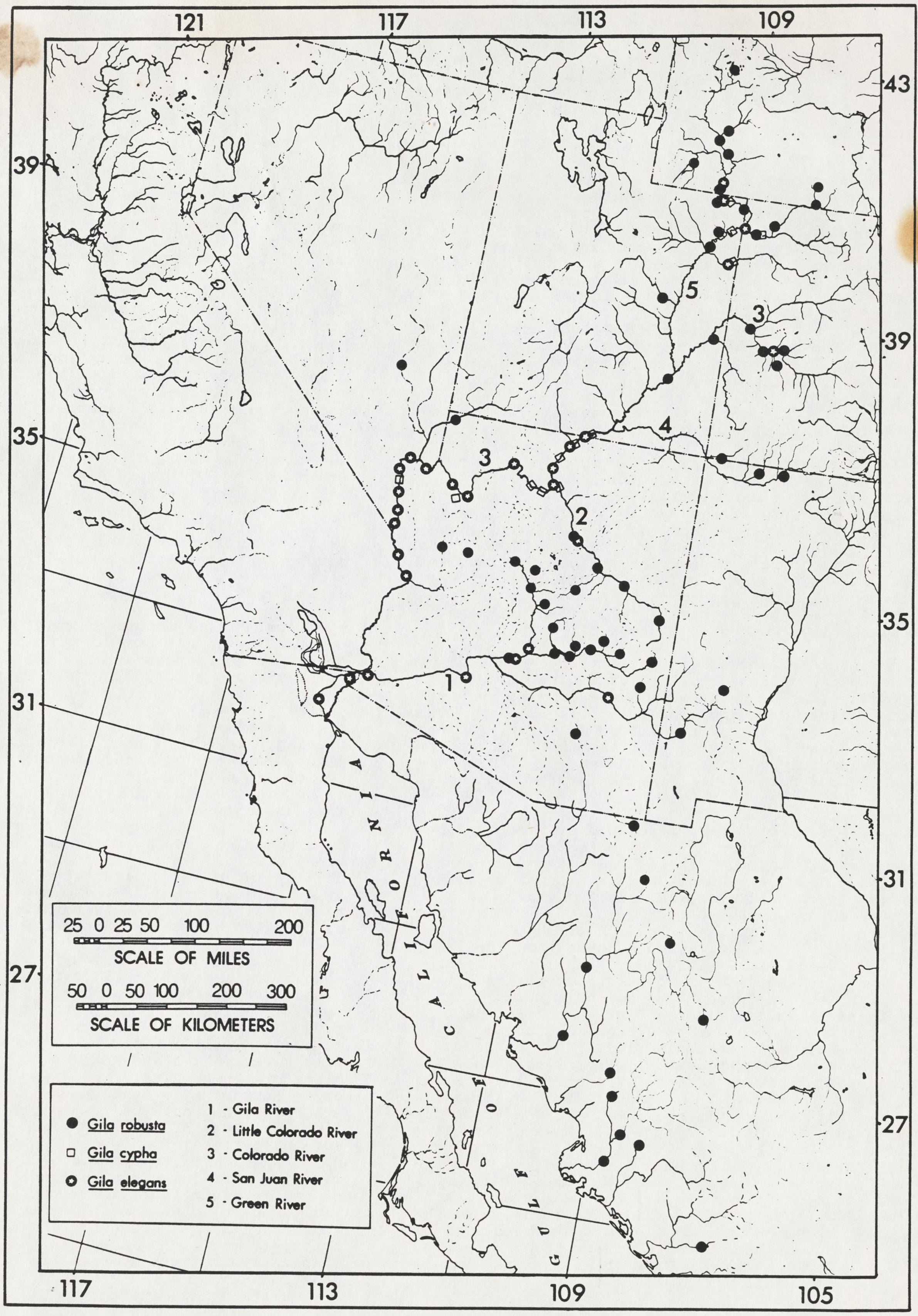

FIGURE 1. Distribution of *Gila robusta*, *Gila elegans*, and *Gila cypha*. See Rhine (1976) for distribution of allied forms in the Gila basin.

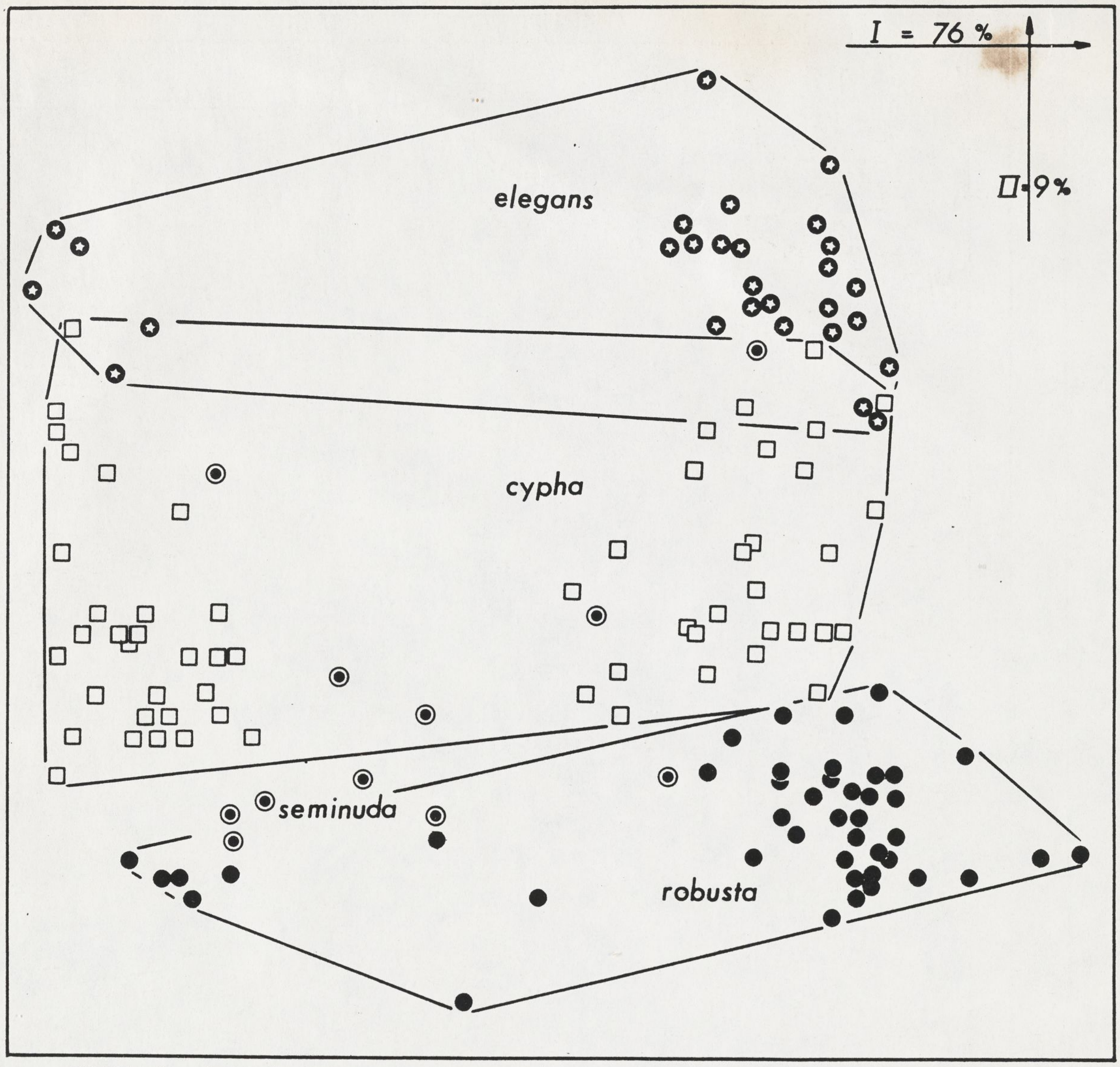

FIGURE 2. Principal components analysis, components I and II, of four forms of *Gila*. *G. robusta robusta*, *G. elegans*, and *G. Cypha* are discriminated by the combination of projections shown in Figure 2 and 3. *G. r. seminuda* is scattered through the other clusters. Percentages indicate the proportion of the total variation accounted for by each component.

TABLE 1. Development of nuchal hump in Colorado River chubs, Genus *Gila*.[a]

Species	Ratio (range)	S.L.range (mm)
cypha (31)	6-13	206-328
elegans (20)	15-29	245-412
r. robusta (17)	28-207	211-309
r. seminuda (4)	31-121	175-247

[a]Expressed as ratio: $\frac{P_1\text{-}P_2 \text{ distance}}{\text{Depth frontal depression}}$.
Figures in parentheses indicate number of specimens measured.

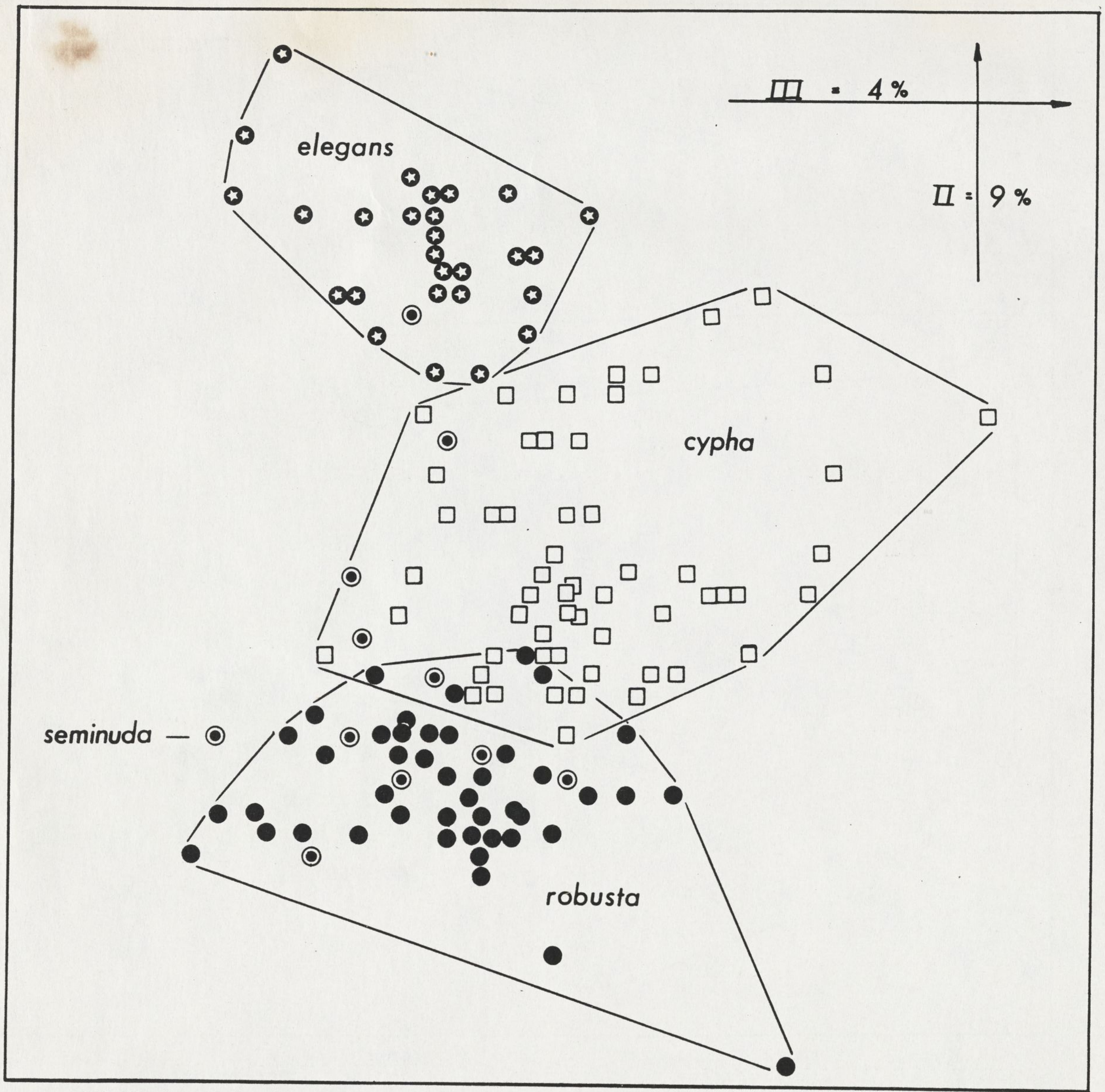

FIGURE 3. Principal components analysis, components II and III, of four forms of *Gila*. Compare with Figure 2.

TABLE 2. Number of gill rakers on second arch in three species of *Gila*.

Taxon	No. of gill rakers											
	12	13	14	15	16	17	18	19	20	21	No.	$\overline{X}$
G. r. robusta	8	13	21	1							43	13.35
G. r. seminuda[a]				4	9	6	4	1			24	16.54
G. cypha		4	13	17	16	4					54	15.05
G. elegans				1	2	8	5	5	3	1	25	17.96

[a]Including the five syntypes, USNM 16975.

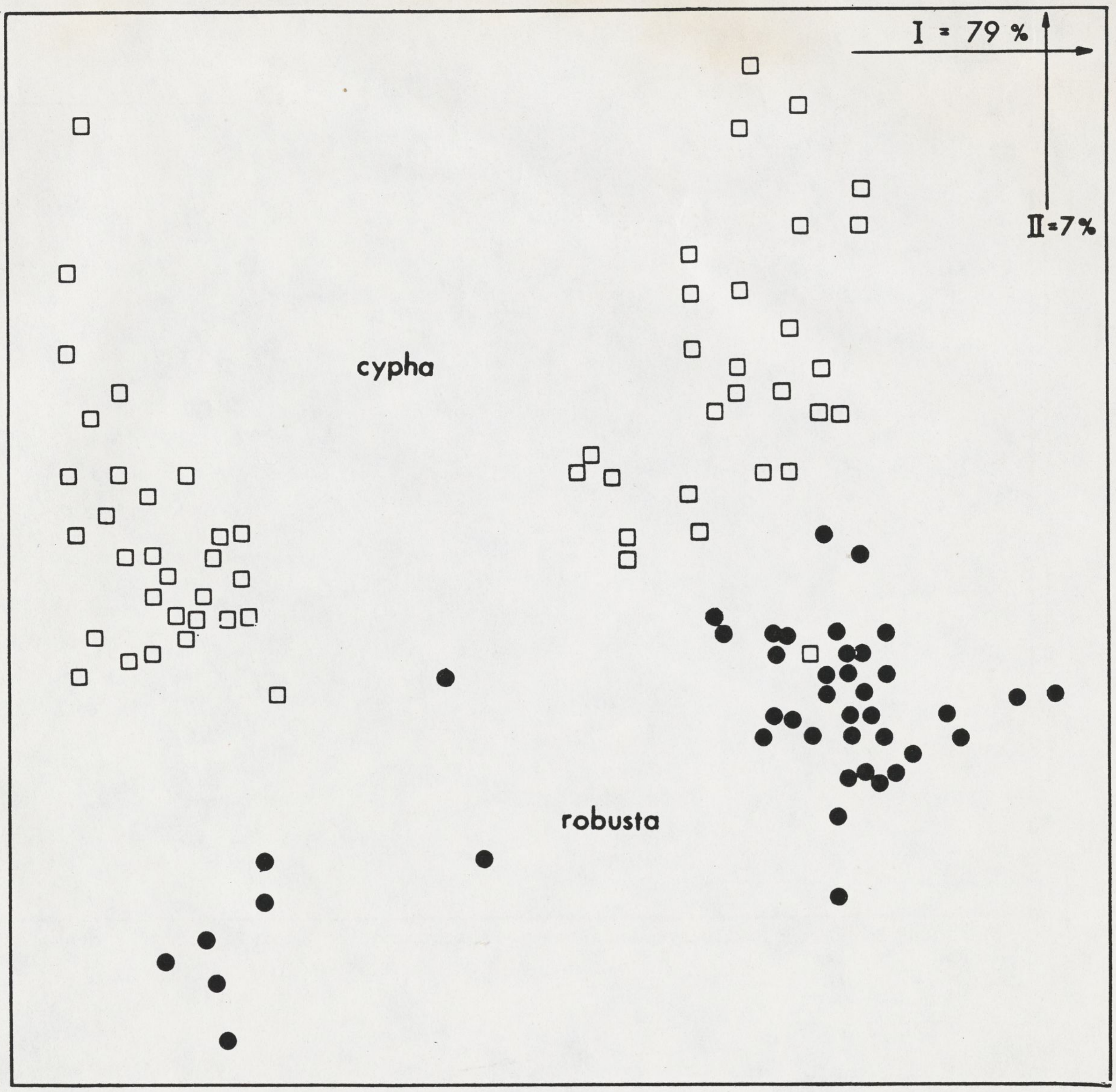

FIGURE 4. Principal components analysis, components I and II, of *Gila cypha* and *G. robusta*. See text for discussion of the specimen of *cypha* in the *robusta* cluster.

TABLE 3. Precaudal vertebrate in Colorado River chubs, Genus *Gila*.

Taxon	Number of precaudal vertebrates[a]								
	18	19	20	21	22	23	24	No.	$\bar{X}$
G. r. robusta	7	43	29	4				83	19.36
G. r. seminuda		2	6	15	10			33	21.00
G. cypha	26	41	25	2	1			95	19.06
G. elegans			1	12	26	9	1	49	21.94

[a]Excluding those in the Weberian apparatus.

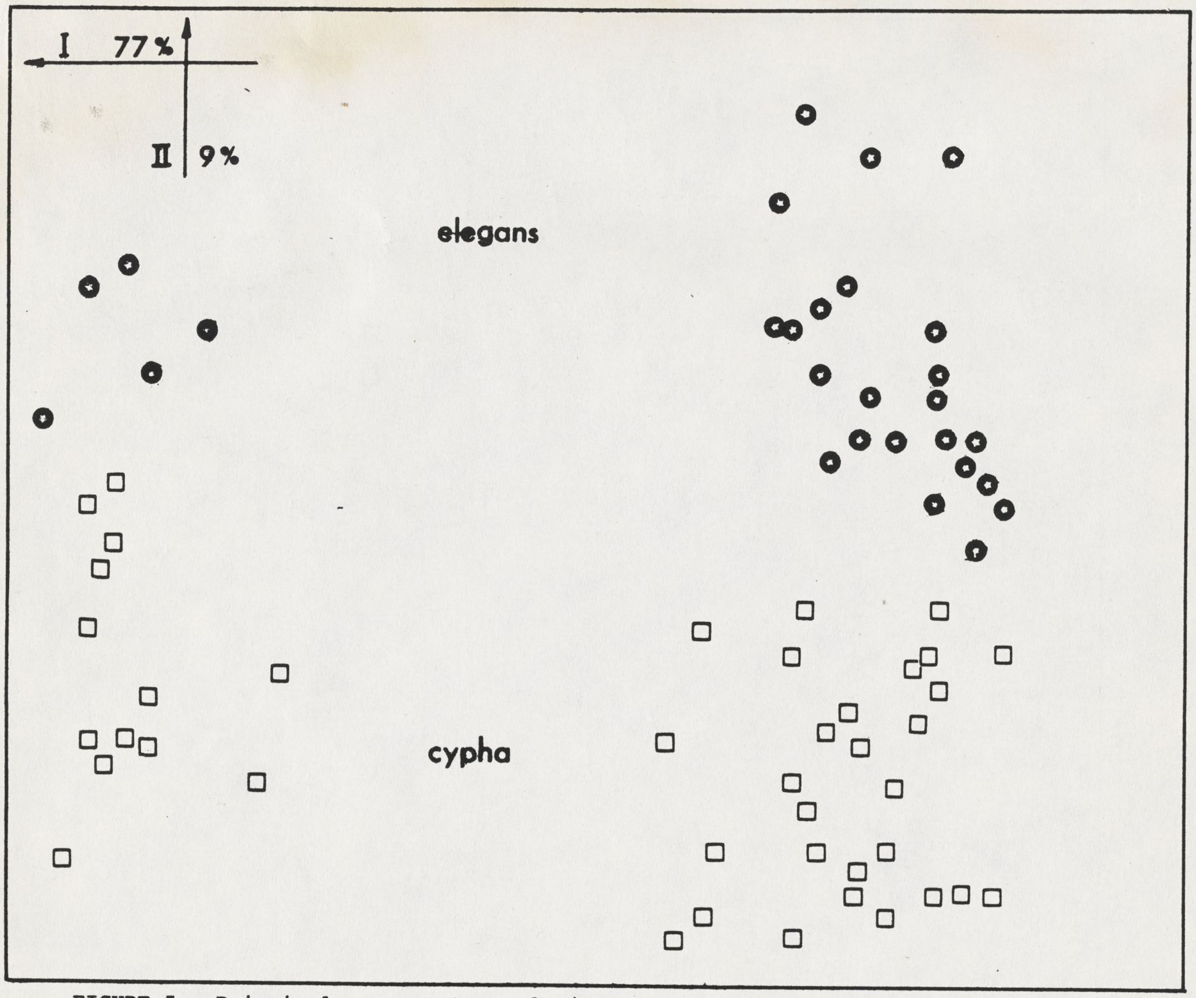

FIGURE 5. Principal components analysis, components I and II, of *Gila cypha* and *G. elegans*.

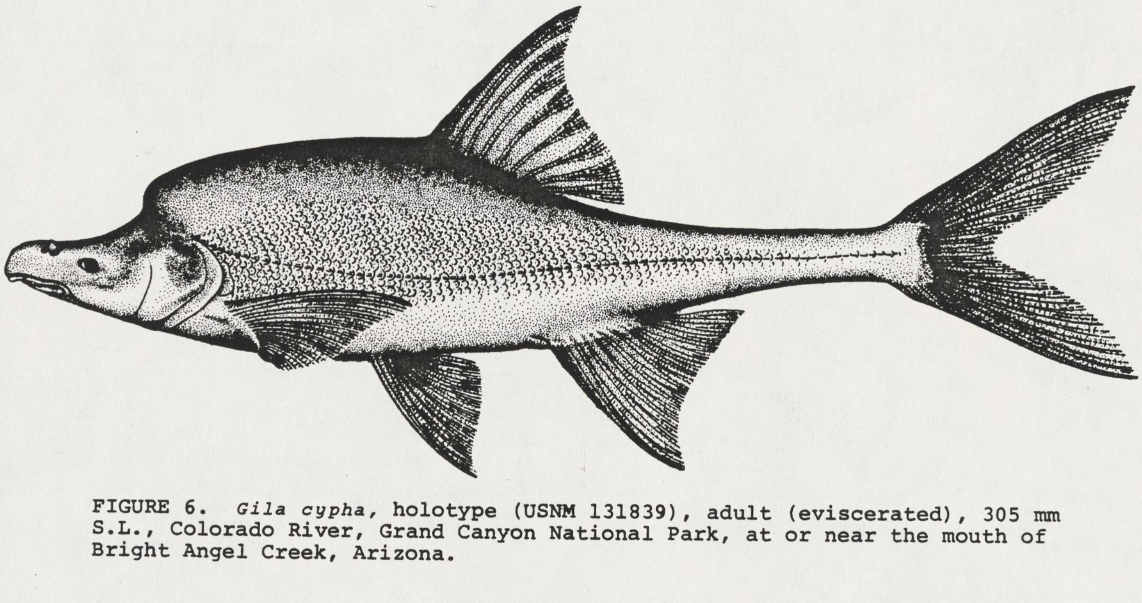

FIGURE 6. *Gila cypha*, holotype (USNM 131839), adult (eviscerated), 305 mm S.L., Colorado River, Grand Canyon National Park, at or near the mouth of Bright Angel Creek, Arizona.

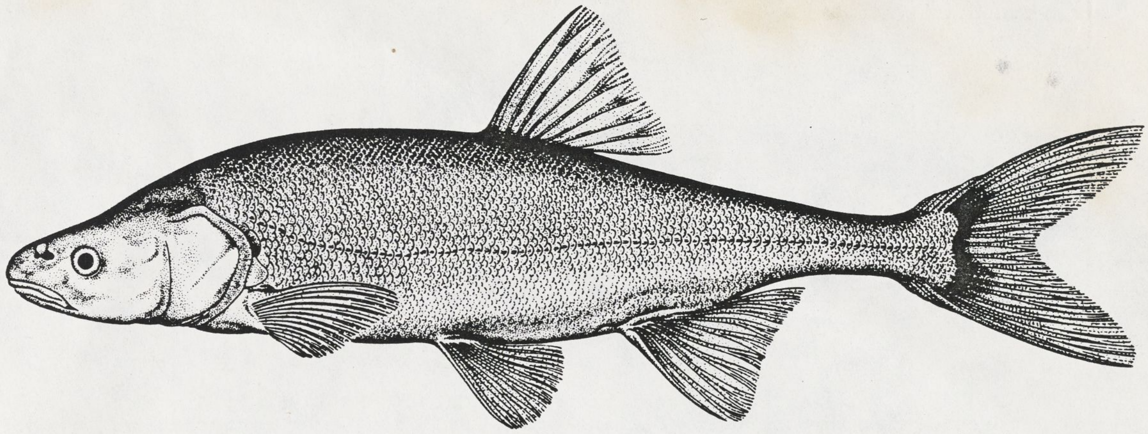

FIGURE 7. *Gila robusta seminuda,* adult female (UMMZ 141666), 189 mm S.L., Virginia River at Littlefield, Arizona.

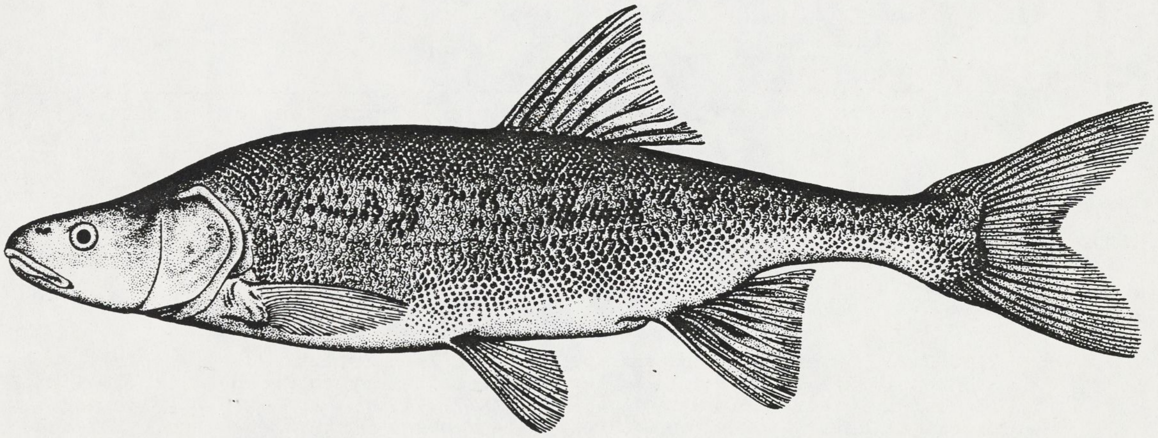

FIGURE 8. *Gila r. robusta,* adult female (UMMZ 182499), 305 mm S.L., Green River about 13 km south of Big Piney, Wyoming.

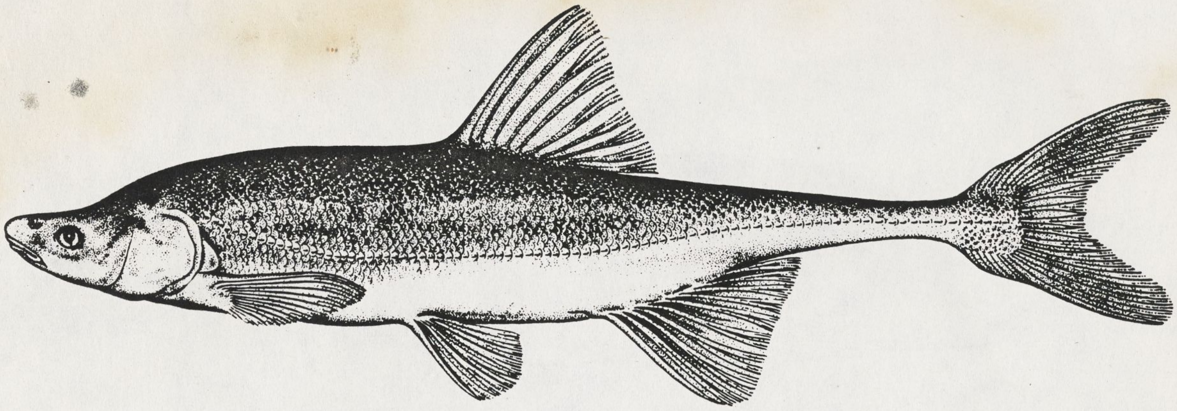

FIGURE 9. *Gila elegans,* post-spawning female (UMMZ 179581), 314 mm S.L., Green River in pool below Flaming Gorge Dam (when under construction), Utah.

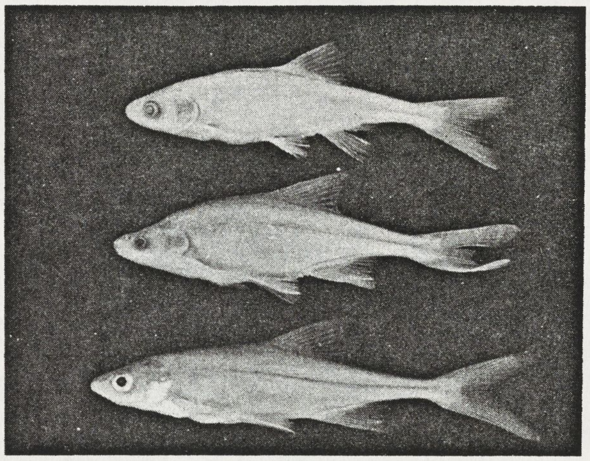

FIGURE 10. Juveniles of three species of *Gila*. (above) *G. r. robusta* (UMMZ 161782), 57 mm S.L., Ashley Creek, tributary to Green River, 16.1 km SE of Vernal, Utah. (middle) *G. cypha* (UMMZ 180090), 58.3 mm S.L., Spencer Creek, tributary to Colorado River, 914 m above mouth, Mohave Co., Arizona. (below) *G. elegans* (UMMZ 94865), 65.3 mm S.L., Gila River below Dome,Arizona. Note snout, concave frontals, small eyes, and intermediate peduncle depth in *cypha*. Note slender peduncle of *elegans*. Counts of fin rays, gill rakers, and vertebrate confirm discrimination of young and adult specimens (see text).

excluding direct measurement of the nuchal hump, is shown in Figure 2. Component I reflects general size; II is especially correlated with numbers of vertebrae, dorsal rays, anal rays, and gill rakers. Figure 3 shows the plot of components II and III of the same analysis. Component III is uncorrelated with II, but is highly correlated with counts of fin rays and gill rakers as well as pectoral length and eye diameter. In the combination of the three axes, which represent summaries of the three major trends in the original 34 characters, *robusta, elegans*, and *cypha* are discriminated with almost no overlap.

Because the status of *cypha* has been most controversial, it was analyzed separately with *robusta* and *elegans*. The discrimination of *robusta* and *cypha*, when these are considered without *elegans* (Figure 4), and of *elegans* and *cypha* alone (Figure 4), shows complete separation for the latter and only a one-specimen overlap between *robusta* and *cypha*. This fish (UMMZ 181281, spec. 2) falls into the *robusta* cluster because it has 9 anal rays (a character of *robusta* weighted strongly by this multivariate analysis) and several other traits that lean toward *robusta*; it is noteworthy that this is the only specimen that did not fall into its own cluster and, when discriminated with key characteristics such as nuchal-hump development (which yielded a 9.2 ratio--see Table 1), it is typical of *cypha*. Moreover, when treated with the other two species together, (Figures 2-3) it also was identified with *cypha*. We cannot be sure, however, that the several traits aligning it closely with *robusta* may not indicate that some *robusta* genes were present in this specimen.

Thus, although some of the individuals falling at or within the borders of clusters (Figures 2-5) could possibly be interpreted as hybrids, the clusters are quite distinct, indicating genetic differentiation and strong reproductive isolation among the three populations in the big-river habitat. The differentiation and isolation are probably facilitated by different ecological roles and habitat preferences within the complex big-river habitat, although insufficient data are available to be certain at this time.

The characters that contribute most to the above clustering are dorsal- and anal-ray number, gill-raker and vertebral-number, and depth and length of the caudal peduncle. *Gila robusta* and *cypha* separated primarily on counts of fin rays, vertebrae, lateral-line scales, gill-rakers, and post-anal length (II). *Gila cypha* and *elegans* separated on correlation patterns dominated by the same characters, excluding pelvic rays and post-anal length, but including snout, eye, and caudal peduncle dimensions. These characters can be used as key characters, but it is interesting that when used alone they do not provide as complete discrimination as do all 34 traits.

Figures 2 and 3 show the position of eleven specimens of *Gila robusta* from the Virgin River, plotted with the clusters of *robusta, elegans*, and *cypha* to demonstrate the nature of overlap of peripheral populations. The Virgin River population is clearly a single variable population with individuals that span some of the variation shown by *robusta, elegans*, and *cypha*. None of the Virgin River specimens have distinct humps, yet their body proportions may be similar to those of members of the other populations in analyses excluding the hump character. This is interpreted as indicating that environmental conditions in the medium-sized tributaries are selecting for some kind of variable average of the three morphotypes present in the large-river habitats, but that the range of heterogeneity of habitat in the medium-sized river is not sufficient to support three separate species. The populations in the medium-sized rivers, for example, the Virgin and the San Juan, are interpreted as adapted to their local environments, and not as intergrades (in the introgressed sense), though limited introgression over the past tens of thousands of years cannot be ruled out. When gill-raker number is considered (Table 2), the Virgin River chub separates well from populations of *Gila robusta* inhabiting the main river.

The results of the above analyses suggest that three populations in the main Colorado River are morphologically segregated and are behaving as reproductively isolated species. Exceptional circumstances exist in peripheral tributaries, for example, the Virgin River, as mentioned above, and possibly in disturbed habitats, such as artificial Lake Powell. These will be mentioned again in the discussion.

The search for key characters to discriminate the above populations involving univariate analysis of a larger sample of 261 individuals. The development of the nuchal hump, as expressed by means of a special ratio (see below), was analyzed in 72 individuals.

One of the impediments to key discrimination of these fishes is the variability and lack of complete discriminating power of the nuchal-hump and caudal-peduncle characters. These traits are obvious and striking and one would like to be able to use them to discriminate the populations, but difficulties in quantification of the nuchal-hump characters have heretofore prevented its effective use. Previous multivariate analyses have included subjective scores for nuchal-hump development, raising the question of subjective influence on the final results.

We have circumvented this dilemma by adapting an instrument described by Eschmeyer and Poss (1977). It provides a direct, repeatable measurement, accurate to 0.1 mm, of the development of the nuchal hump in association with the depressed (often concave) dorsal surface of the skull, features most conspicuous in *Gila cypha* (Figure 6). A ratio derived by measuring the depth of the frontal depression (the maximum distance between a straight line from highest part of nuchal hump and dorsal tip of snout, and dorsal surface of skull) and dividing this figure into the distance between the insertion of the pectoral and pelvic fins, provides an effective means for distinguishing adults of the three chubs of the middle and upper Colorado River basin (Table 1).

Number of precaudal vertebrae (Table 3) proves to be useful, along with gill-raker number (Table 2), in discriminating *Gila robusta seminuda* Cope (Figure 7), from the typical subspecies, *G. r. robusta* (Figure 8). Counts of these vertebrae provide a better separation than the total number which (excluding Weberian vertebrae) varies from 40 to 45, modally 42, in *seminuda*, and 39 to 44, modally 42, in *robusta*. *Gila r. seminuda* is closest to *G. elegans* (Figure 9) in number of precaudal vertebrae, as well as in gill-raker number, but separates well from that species on the basis of nuchal hump development (Table 1) although more and (especially larger) individuals need to be examined to verify this. Modally, *G. robusta* has nine dorsal and anal rays; *G. cypha* usually has nine dorsal and 10 anal rays; and *G. elegans* has 10 dorsal and 10 or 11 anal rays. *G. r. seminuda* tends to be intermediate.

DISCUSSION

Our analyses indicate that *Gila robusta, cypha*, and *elegans* coexist as three separate, reproductively isolated species in the main channels of the Colorado and Green rivers. This conclusion cannot be confidently applied to certain populations that we have available but have not fully studied from Lake Powell, however. Furthermore, populations of *Gila robusta* from certain tributaries were *elegans* and *cypha* are absent parallel these species in many characteristics. We choose a taxonomic treatment of this situation that emphasizes the specific distinction of the three populations in the big-river habitat, but admit the possibility that the species isolating mechanisms may break down under disturbed (reservoir) conditions and that the populations in tributary streams may not be completely independent or isolated from the three central forms. We refer to the entire complex as the *Gila robusta* superspecies, including *robusta, cypha,* and *elegans* as defined above, and including subspecies or races of *robusta, seminuda* of the Virgin River, a similar population in the San Juan River, and a number of isolated populations in northern and western Mexico. The complex in the Gila River basin includes *Gila intermedia* and forms intermediate between that species and *robusta,* i.e., *G. r. "grahami"* (cf. Rinne, 1976). *Gila intermedia* is inferred to be a part of the *robusta* superspecies on the basis of shared characters and possible gene exchange through *"grahami"*, but may be a sister phyletic line by its origins, as indicated by its similarity to several of the large-scaled, small-finned subgenera of *Gila* (cf. Miller, 1945).

In spite of the uncertainty regarding peripheral populations, it is clear that *robusta* (s.s.), *elegans,* and *cypha* have diverged in a number of characters, and can be discriminated on the basis of counts of fin rays, vertebrae, and gill rakers, the relative depth and length of the caudal peduncle, snout shape, fin position, and form of the nuchal hump. The multivariate analysis shows that *cypha* is intermediate between *robusta* and *elegans* in general, but is extreme in several respects. This suggests the possibility that *cypha* and *elegans* were derived from *robusta* by separate speciation events. *Gila robusta* shows the most primitive characters of the three, and the separate ways in which *elegans* and *cypha* are extreme suggest that neither is likely to be ancestral to either of the other two.

The lack of coexistence of the three species in smaller tributaries is in accordance with the expected relationship between diversity and spatial heterogeneity. The species seem to be omnivorous carnivores with specializations related to habitat --chacters associated with food processing (jaws, teeth) are similar, except that *robusta* has fewer gill rakers and *elegans* more (Table 2). In small tributaries, such as the Virgin and possibly the San Juan, a single species with intermediate morphology seems to be selected for; in the larger tributary systems of the Gila River, a bewildering mosaic of generalized forms occur (Rinne, 1976), where in former times *robusta* and *elegans* lived in the main channel.

The close apparent control of habitat size and diversity over morphology and species diversity suggests that if the habitat could be experimentally changed, the populations should show predictable responses. Rather unfortunately, the destruction of main-river habitat by Glen Canyon Dam has created such an experiment. Early indications are that the two more specialized species will not exist in the Lake Powell environment. The three species seem to be breaking down locally by hybridization. We predict that a single-species of mixed origins and generalized characteristics will appear. Given long enough, some re-oriented diversification would develop, but the reservoir is apparently silting in too rapidly for the necessary stability to persist.

In a period of controversy following the poisoning of the upper Green River in 1962 (Miller 1963b), erroneous statements about the classification, biology, and distribution of Colorado River chubs appeared which have been destructive to the understanding and management of these fishes, and require correction. For example, Stroud (1963:7) irresponsibly claimed that the construction of Flaming Gorge Reservoir resulted in making available "large numbers" of humpback chubs, all of which were supposedly males. The agency (U.S. Bureau of Sport Fisheries and Wildlife) that "confirmed the presence and ready availability of numerous humpback chubs in [the Green River below Flaming Gorge Dam] . . ." subsequently reported (Vanicek 1967; Vanicek et al. 1970; Holden and Stalnaker 1975) the absence of *Gila cypha* in the area indicated and great rarity of this species below the mouth of the Yampa River; only three specimens were taken in 1963, and none during 1964-1966, in the Green River in Colorado and Utah (Kramer 1967:Table 2; Vanicek et al. 1970:Table 4).

Vanicek and Kramer (1969:194-195) stated, ". . . criteria are not available for distinguishing between young fish of the two morphological variants" (i.e., between what were then called *Gila r. robusta* and *G. r. elegans*). "Consequently, specimens shorter than 200 mm total length were combined in the present study under the general taxon, Colorado chub." Collections of *Gila robusta* and *G. elegans* at The University of Michigan, containing young as small as 22 to 40 mm S.L., were identified as early as 1926; by 1968, humpback chubs as small as 43 mm S.L. had been determined. By the criteria reported here, we have identified *Gila robusta robusta* (UMMZ 162818) to 20 mm, *Gila cypha* (UMMZ 182415) to 54 mm, and *Gila elegans* (UMMZ 162846) to 22 mm in total length. Juveniles of three species are shown in Figure 10. Holden and Stalnaker (1975) (citing Minckley and Deacon, 1968, as authority) reported Colorado squawfish (*Ptychocheilus lucius* Girard) in the Grand Canyon, but the two specimens actually came from between Glen Canyon Dam and Lees Ferry, well above Grand Canyon. The only valid record (based on preserved material) known to us of this species from the Colorado River in Grand Canyon is represented by an adult (about 320 mm S.L.) caught in 1975 by an unknown fisherman at the mouth of Havasu Creek (ASU 7087). However, squawfish formerly moved up the Little Colorado River in Grand Canyon to the base of Grand Falls (Miller, 1963a:1, ftn.1).

In our distribution map of the *Gila robusta* complex (Figure 1), the record for *G. elegans* in the Little Colorado River (at base of Grand Falls) is based in part on the statement referred to above, in part on our conclusion as to the true type locality for *Gila elegans* (and *Gila robusta*), and in part on the absence of the bonytail from the Little Colorado River above Grand Falls. The holytype (USNM 251), as well as the three syntypes of *Gila robusta* (USNM 246), were said to have come from the "Zuni River, New Mexico" (Baird and Girard, 1853, 1854; Girard, 1858:286-287). However, at the time of collection during the summer (rainy season) of 1852, Zuni River was described ". . . as a mere rivulet, and not entitled to the name of river; in most parts of our country it would not be dignified with that of creek" (Sitgreaves, 1854:5). This is hardly the habitat of *Gila elegans* and, moreover, that species is unknown from the Little Colorado River basin (to which Zuni River is tributary in floods) above Grand Falls, an impassible barrier 56 meters high (Dryer, 1965). Furthermore, careful examination of the channel of Zuni River in New Mexico convinced us that (at least in recent centuries)

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CENOZOIC FRESHWATER FISHES OF NORTH AMERICA

◆4191

Gerald R. Smith

Museum of Paleontology and Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109

INTRODUCTION

Comparison of fossil and Recent fishes reveals patterns of evolution related to changing geography and environments. Historical comparison of the fish faunas of eastern and western North America leads to the conclusion that barriers and long-term stability of aquatic habitat are the most important factors controlling species density and broad patterns of evolution. The perspective offered by paleontological evidence is useful because, although neontological samples are rich in anatomical and ecological detail, historical inferences based on them are usually chronologically inaccurate. Our tendency to ascribe events to important recent circumstances—geologic, geographic, or cladistic—results in a bias toward interpretations postulating rapid rates and relatively recent causes. In fact, changes in species are generally much slower than changes in geography and climate, and therefore we cannot assume that fishes have recently adapted to the environments and climates in which they presently live.

The scope of this review includes freshwater fishes in North America north of Mexico in Miocene, Pliocene, and Pleistocene sedimentary rocks. I emphasize middle-latitude faunas, which are better known and have richer fossil representation than those of glaciated latitudes. Fossil fishes preserved in freshwater deposits are conveniently separated both ecologically and, for the most part, phylogenetically from those in marine environments with little ambiguity. The dominant families of freshwater fishes in the late Cenozoic of North America are the gars (Lepisosteidae), trouts and salmon (Salmonidae), pikes (Esocidae), minnows (Cyprinidae), suckers (Catostomidae), catfishes (Ictaluridae), pupfishes (Cyprinodontidae), perch (Per-

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cidae), sunfish and bass (Centrarchidae), [illegible]ulpins [illegible] sticklebacks (Gasterosteidae). The species representing these [illegible] eral other families in the fauna are itemized in Tables 1 an[illegible]

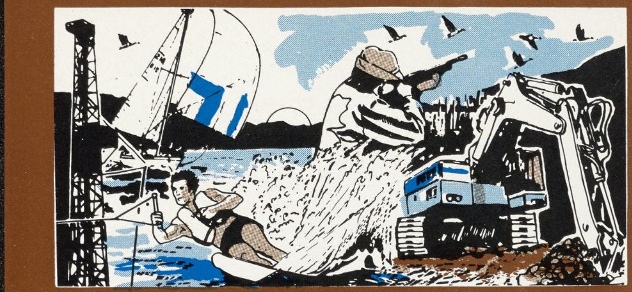
During the first half-century of research in this small disci[illegible] all of the work was done by E. D. Cope, whose researches b[illegible] and 1896 touched upon most of the important Cenozoic faunas [illegible] discovered later in Kansas and Nebraska. Many of his interpret[illegible] stand, except that later workers have been unable to recognize [illegible]any genera and species.

Most of the 20th century research in this field, culminating in the m[illegible]jor reviews by Miller (87, 88) and Uyeno & Miller (144), has bee[illegible] work of R. R. Miller and C. W. Hibbard and their students. C. L. Smith described most of the fishes in Claude Hibbard's Pliocene and Pleistocene faunas f[illegible] the high plains, and pioneered climatic inference based on fish distribu[illegible] (112–116). T. Uyeno contributed most to our knowledge of fossil Cy-prinidae (140) and (with Miller) Cyprinodontidae (143). The most impor[illegible] tant recent advances are the cladistic monographs by Lundberg (78) on catfishes (Ictaluridae), Wiley (148) on gars (Lepisosteidae), and Boreske (12) on Amiidae. The project summarized here is a continuation of work begun by C. W. Hibbard and R. R. Miller in the Snake River Plain and the Great Basin.

Studies of Cenozoic fossil fishes have been largely descriptive natural history, with almost no theoretical contributions emerging from Cope's contributions or those presented in the framework of the New Systematics. Reconstruction of past environments, hydrography, and dispersal, as well as documentation of species occurrences in relation to stratigraphy, have been (and continue to be) primary objectives. Stanley's (128) challenge to traditional views represents the first major theoretical use of the data. Stanley focusses our attention on whether most evolutionary changes are associated with cladogenesis. The history of North American fishes suggests that we must also examine the effects of stability and barriers on extinction, evolution, and speciation.

DISTRIBUTION AND DRAINAGE

At middle latitudes in the United States, Pliocene to Recent fish faunas are sharply divided by the Rocky Mountains into a species-rich component centered in the Mississippi basin in the east and a depauperate element scattered through the western basins (87). To the southwest and into Mexico the fauna is a mixture of these two together with endemic and Central American groups (90, 125–127). The vast glaciated areas of the northern part of the continent were colonized 17,000–8000 years ago from middle-



JUNIPER-CROSS MOUNTAIN

1980
1981

A WESTERN COLORADO PROJECT

Juniper-Cross Mountain is a proposed two dam and reservoir project west of Craig on the Yampa River in Northwest Colorado. It will produce 350 million kilowatt hours of electricity annually, store almost 1.3 million acre-feet of water, accommodate 500,000 recreation days per year and has the potential to irrigate 18,000 acres directly and more by exchange. Total project cost will be paid by water and power sales revenue; there are no state or federal funds involved. The first land set-aside for the project was made in 1905 and federal power site withdrawals were made subsequently. Sponsors of the project are Colorado-Ute Electric Assn., which will own the transmission system and has expressed an intent to purchase project power, and the Colorado River District, which will own the dams and reservoirs.

Colorado-Ute is a non-profit corporation organized to supply all power needs to 13 rural electric cooperatives in Colorado. The 15-county Colorado River District was created by the state legislature in 1937 to safeguard, conserve and put to beneficial use the waters of the Colorado River Basin for Colorado. A project license application is pending before the Federal Energy Regulatory Commission. The application proposes start of construction on Juniper Dam in January, 1982, start of Cross Mountain Dam construction in 1983 and filling of both reservoirs by 1985.

Those wanting more information about the project or who wish to help in getting the project under construction should contact the River District.

COLORADO RIVER WATER
CONSERVATION DISTRICT
GLENWOOD SPRINGS, COLORADO
303/945-8522 / P.O. BOX 1120 / 81601

JUNIPER DAM AND RESERVOIR SPECIFICATIONS

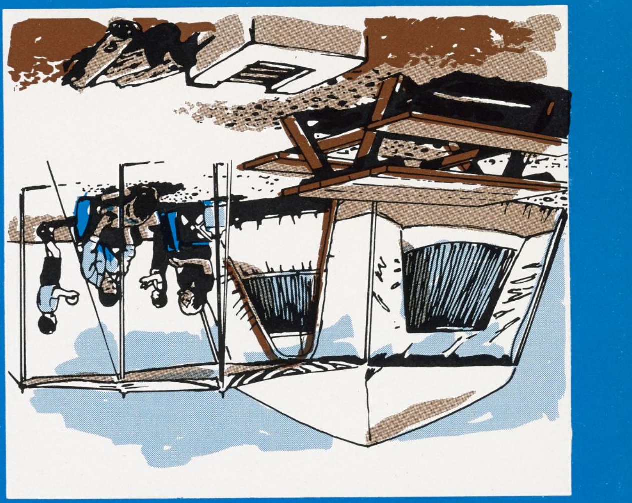
Dam height	220 feet
Dam type	rockfill
Location	25 miles southwest of Craig
Water storage capacity	1,082,000 acre-feet
Active storage	692,000 acre-feet
Installed capacity	98,000 kilowatts
Average annual production	158,500,000 kilowatt hours
Maximum discharge	7,000 cubic feet per second
Minimum discharge	25 cfs
Spillway capacity	134,900 cfs
Average annual evaporation	43,800 acre-feet
Shoreline	114 miles
Water surface area	15,375 acres
Land surface area	2,543 acres
Maximum water surface elevation	6,125 feet

CROSS MOUNTAIN DAM AND RESERVOIR SPECIFICATIONS

Dam height	260 feet
Dam type	concrete arch
Location	58 miles west of Craig
Capacity	208,000 acre-feet
Active storage	115,000 acre-feet
Installed capacity	50,000 kilowatts
Average annual production	190,400,000 kilowatt hours
Maximum discharge	3,000 cubic feet per second
Minimum discharge	200 cfs
Spillway capacity	96,000 cfs
Average annual evaporation	19,700 acre-feet
Shoreline	55 miles
Water surface area	6,700 acres
Land surface area	2,617 acres
Maximum water surface elevation	5,888 feet

Going forward with

JUNIPER-CROSS MOUNTAIN



A RECREATIONAL PARADISE

With its narrow canyons, wide lakes, long but irregular shorelines and limited access to isolated areas, Juniper-Cross Mountain will be one of the most popular outdoor recreation centers in the Rockies. Most of the recreation features have been sited in conjunction with topography, vegetation and special scenic features.

Fishing potential is excellent; the reservoirs can be managed as cold or warm water fisheries or a combination of the two with species such as rainbow trout, coho salmon, walleye and bass likely. An annual harvest of 250,000 pounds is projected.

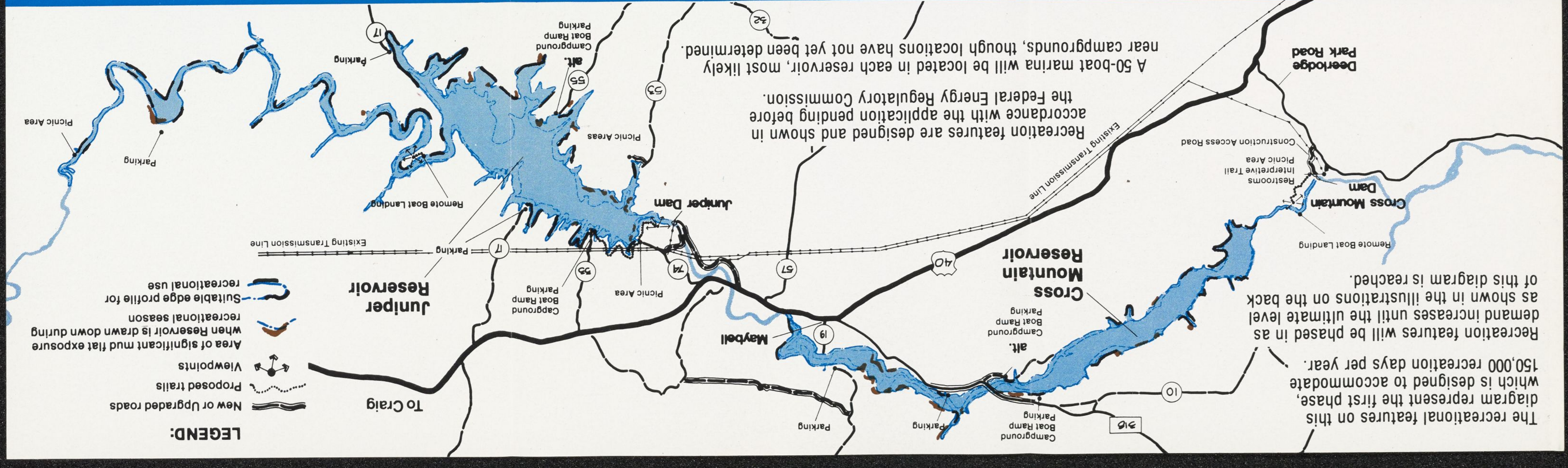
Currently there is little boating or fishing in the project area. Most of the river boating activities on the Yampa River occur in Dinosaur National Monument, where, according to the Park Service, approximately 20,000 boating days per year are experienced. Although the operating plans for

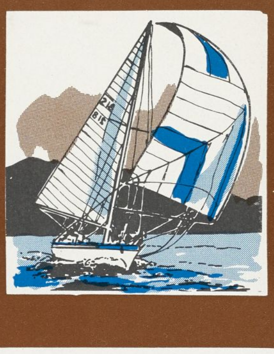
Juniper-Cross will increase low flows and probably lengthen the rafting season, the project will also moderate high flows. This may be perceived as diminishing the rafting experience for some downstream boaters, while the reservoir creates new opportunities for 500,000 recreation days at the project.

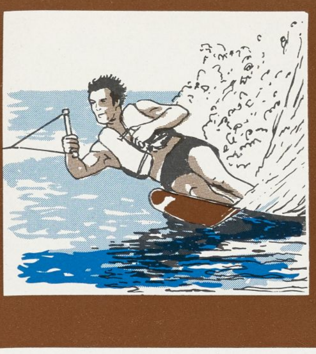
With warmer waters, more gradual shorelines and better water quality than most major reservoirs, Juniper and Cross Mountain will provide fine swimming and water skiing opportunities during the summer. Ice fishing, skating and snowmobiling should prove popular during the winter.

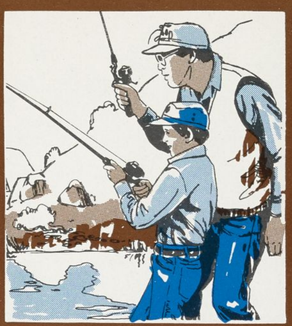
Each reservoir will have a boat ramp, marina and boat landing for access to scenic features. There will be 26 miles of trail leading to such areas as Cross Mountain Canyon rim, Signal Butte and Little Juniper Mountain and taking off from a campground, picnic area or boat landing.

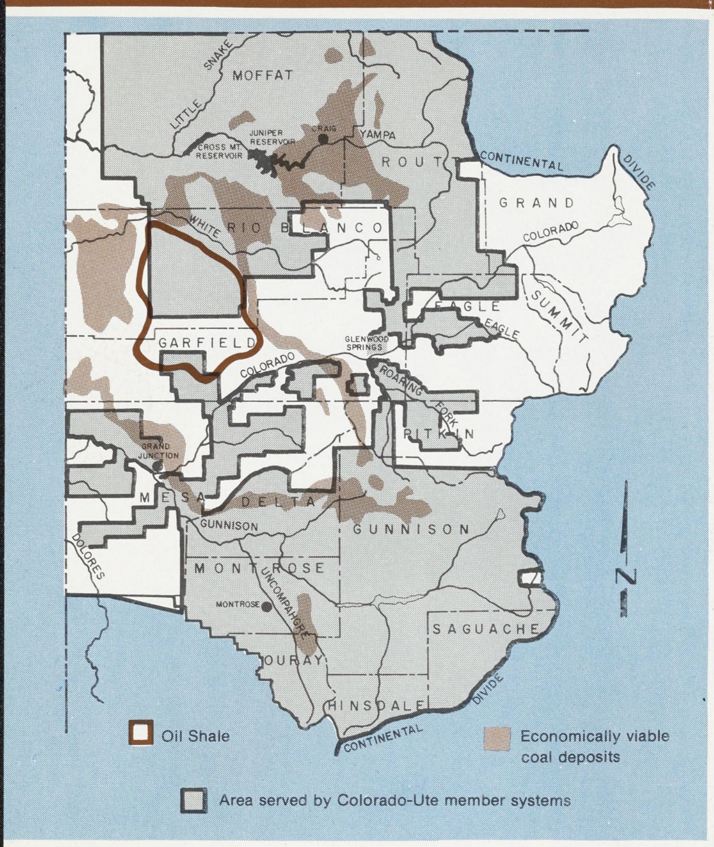
Special emphasis will be given hiking and nature trails through the previously inaccessible but spectacular scenery of the project area.











AIDING ENERGY DEVELOPMENT

Juniper-Cross will produce 350,000,000 kilowatt hours annually of renewable hydroelectric power that generates neither air nor water pollution. It will not only replace the equivalent of 600,000 barrels of foreign oil, but much of its production will be the more critical peaking power. Northwest Colorado contains some 40 billion tons of coal, one trillion barrels of shale oil and substantial oil, gas and uranium deposits. The water supply, power production and recreational features of the project will significantly assist the growing energy industry and its workers.

ENVIRONMENTAL ACCORD

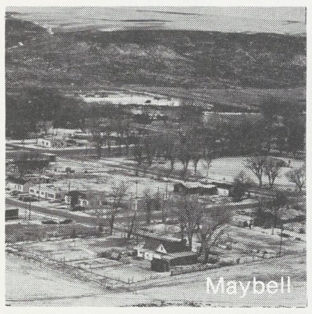
Some $3 million has been proposed for a wide range of features that would enhance the environment, mitigate potential impacts from the project and develop and preserve a record of the area's history. Cross Mountain releases will increase average low flows thus expanding fish habitat downstream of the project and improving reproduction of several fish species. The inactive portion of Juniper Reservoir will hold 350 years of river sediment eliminating silt as a factor in Cross Mountain Reservoir and substantially reducing the river's silt load and improving water quality downstream of the project. Sole source of air, noise or water pollution through the life of the project will be limited to that generated by recreation users. Detailed archaeological and paleontological studies are a part of the pre-construction process and will aid in the establishment of a collection of artifacts and history from the area that will be included in the Cross Mountain Interpretive Center. Through the design and planning of Juniper-Cross Mountain, special care has been taken to place features in harmony with the project's environment.

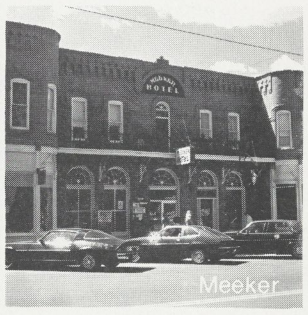
WATER FOR LIVING THINGS

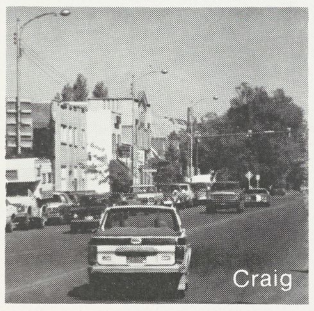
Colorado's third largest river, the Yampa, is a life-giving thread for people, plants and animals in a 7,200 square-mile basin. Control of the project's water supply by the River District, a regional Western Colorado water agency, allows for use of project water to satisfy downstream requirements, to provide for increased upstream water use by exchange, and to generally ease drought conditions in Western Colorado. Though not designed as a flood control project, Juniper-Cross will reduce the severity and frequency of floods downstream. Juniper-Cross has the potential to irrigate 18,000 new acres of land and to provide supplemental water for irrigated lands that run short in late season. Juniper-Cross will also ease the pressure on agricultural water brought about by increasing demands from municipalities and energy industry users.

DIVERSIFYING AN ECONOMY

The diversification of Northwest Colorado's energy-agriculture-tourism economy will be strengthened by Juniper-Cross Mountain. Based on existing travel patterns and a comparison with similar projects, the engineering, cultural and recreational features of Juniper-Cross will ultimately generate 500,000 visitor days per year. Economic benefits from tourism as a result of the project are expected to center in Craig, Meeker and Steamboat Springs and spread to communities on major travel routes such as Rifle, Glenwood Springs, Grand Junction, Delta, Rangely and Hot Sulphur Springs. About 67% of the project's estimated $185 million cost will probably be spent in the region. Total economic benefit to the region based on tourism and other uses will exceed several million dollars annually.







With a rich history steeped in ranching, Maybell, Meeker and Craig are the community neighbors to Juniper-Cross. Meeker and Craig are in varying stages of substantial growth brought about by major coal and oil shale development projects.

JUNIPER-CROSS MOUNTAIN

The proposed Juniper-Cross Mountain Hydroelectric Project, west of Craig on the Yampa River in Northwest Colorado, represents major opportunities for the region in terms of water for the city of Craig and agriculture, recreation and power production. Total estimated 1980 project cost is $185 million. The project will provide Moffat County and the region with recreational benefits or economic gains in tourism valued at several million dollars a year. There are no state or federal tax monies involved — the project will be paid for with revenue from the sale of power. A license application is currently pending before the Federal Energy Regulatory Commission. Following is a discussion of related issues or those normally raised on such water projects.

FREE-FLOWING * * * * * * * * * * EVAPORATION

IRRIGATION * * * * * * * * * * * * * WATER SUPPLY

SILT * * * * * * ARCHEOLOGY/PALEONTOLOGY

LAND USE * * * * * * * * * * * * * * * * * MITIGATION

* * * * * * * * * HISTORIC ECHOES * * * * * * * * *

CROSS MOUNTAIN * * * * * * * * * * * * * SALINITY

EXISTING RECREATION * * * SELECT SPECIES

FUTURE RECREATION * * * LAND ACQUISITION

POWER VALUES * * * * * * * * * * WILD & SCENIC

FREE-FLOWING

The Yampa River, third largest in Colorado, is many things. It is a life-giving thread to people, plants and animals in a 7,200 square-mile basin. It ranges in elevation from 12,000 feet near its headwaters in the mountains where most of the flow originates from snowmelt to 5,000 feet about 25 miles below Cross Mountain Dam where it joins with and becomes the Green River. While an average of one million acre-feet annually flows in the Yampa River, an average of only 10 inches of precipitation annually falls at the lower elevations. And while the Yampa is a lot of things to a lot of people, one thing it is not is a so-called free-flowing river. The Yampa has four dams across its main stem that total 23,812 acre feet of storage: Lake Catamount, Stillwater Number 1, Upper Stillwater and Yamcolo reservoirs. In addition, the main stem has 150 diversion structures from the headwaters to the confluence of the Little Snake River with absolute water decrees totaling approximately 1,700 cubic feet per second or some 3,372 acre-feet per day. Owner of the greatest amount of storage in the basin is the Colorado Division of Wildlife.

EVAPORATION

Evaporation is a fact of life in water storage reservoirs. Except in closed receptacles, water cannot be stored without an evaporation factor. Projects constructed and proposed under the Colorado River Storage Project Act, Eastern Slope projects and storage reservoirs related to transmountain diversions all have an evaporation factor. Juniper-Cross is no different.

The evaporation factor on Juniper-Cross Mountain is a net 2.8%. In other words, in order to use 97.2% of water flowing into the reservoirs, 2.8% must be expended in the form of evaporation.

More refined studies of evaporation losses for Juniper-Cross indicate a mean annual net evaporation loss of 38,200 acre-feet. Average annual evaporation loss from the river reach in its present state totals about 2,000 acre-feet for a total net evaporation loss with the project of 36,200 acre-feet. The ratio of acre-feet of evaporation to acre-feet of storage on Juniper-Cross is comparable to several constructed and many other potential reservoirs in Western Colorado such as Dominguez and Una.

FREE-FLOWING * * * * * * * * * * EVAPORATION

IRRIGATION * * * * * * * * * * * * WATER SUPPLY

SILT * * * * * * ARCHEOLOGY/PALEONTOLOGY

LAND USE * * * * * * * * * * * * * * MITIGATION

* * * * * * * * HISTORIC ECHOES * * * * * * * *

CROSS MOUNTAIN * * * * * * * * * * * * SALINITY

EXISTING RECREATION * * * SELECT SPECIES

FUTURE RECREATION * * * LAND ACQUISITION

POWER VALUES * * * * * * * * * WILD & SCENIC

IRRIGATION

The Juniper-Cross Mountain Project will inundate approximately 4,000 acres of farm land. Independent of the license application pending before the Federal Energy Regulatory Commission, the Maybell-centered Juniper Water Conservancy District and the Colorado River Water Conservation District are co-sponsoring a feasibility study aimed at seeing how much of 30,000 acres southwest of Maybell can feasibly be irrigated with project waters. Several years ago, a Bureau of Reclamation study concluded that these lands, in the Deception Creek area, based on both contours and soils, would definitely produce crops with water.

Preliminary indication from the new study is that sprinklers must be used but that, with sprinklers and efficient practices, Deception Creek lands can produce more crops per acre with less water than the bottom lands that will be inundated. As a part of the new study, soil samples were taken both from the Deception Creek area and from bottom lands near Sunbeam. Those samples were analyzed and determined to be the same. One question still to be answered by the new study is the economic feasibility of the water, pumping and construction costs related to the proposed irrigation system.

WATER SUPPLY

Besides the irrigation potential, project sponsors have entered into an agreement with the City of Craig that will essentially assist the city in having a dependable water supply sufficient to meet current needs and future growth. The two primary points of the agreement are that the Juniper-Cross Mountain Project will strengthen the junior rights on the city's own reservoir and that the city has the right to purchase 10,000 acre-feet from Juniper Reservoir directly or by exchange at a future date.

The contractual agreement between the River District and Colorado-Ute on power production from Juniper-Cross includes a proviso that enables the River District to put the project's waters to other beneficial uses while paying power interference to Colorado-Ute.

With growth projections for both municipal users and energy development in Northwest Colorado, demand for water will increase substantially. Although there are no formal agreements beyond those for irrigation and the City of Craig, the possibility remains that Juniper-Cross waters will be used to fulfill other municipal needs and the need for such energy developments as coal mining and conversion plants.

IRRIGATION * * * * * * * * * * * * WATER SUPPLY

SILT * * * * * * ARCHEOLOGY/PALEONTOLOGY

LAND USE * * * * * * * * * * * * * * MITIGATION

* * * * * * * * HISTORIC ECHOES * * * * * * * *

CROSS MOUNTAIN * * * * * * * * * * * SALINITY

EXISTING RECREATION * * * SELECT SPECIES

FUTURE RECREATION * * * LAND ACQUISITION

POWER VALUES * * * * * * * * * * WILD & SCENIC

SILT

Siltation, or the filling of a reservoir over a period of time with sand and other earth type materials usually carried by a river's flow, is always a consideration in reservoir construction and in determining the useful life of a reservoir.

As designed, the upper reservoir, Juniper, will have active storage of 692,000 acre-feet and inactive storage of 390,000 acre-feet. Based on the present silt load of the Yampa River, it will take 350 years of sediment deposition to fill the inactive portion of Juniper Reservoir – before the active portion becomes impacted. Construction of other upstream reservoirs will decrease sediment and lengthen that period. Furthermore, as a result of settling in Juniper, water flowing into Cross Mountain Reservoir will be clear and siltation in that reservoir will not be a factor. Thus, the normal silt load of the Yampa River upstream of the project will not have any measurable impact on it for a few centuries.

The Little Snake River, which joins the Yampa about five miles below Cross Mountain Dam, is the primary contributor of sediment to the Yampa River. So, while releases from Cross Mountain will essentially be clear, the flow below the confluence with the Little Snake will approximate the Yampa's historic silt load.

ARCHEOLOGY/PALEONTOLOGY

Extensive efforts are already under way to document the history and prehistory of plants, animals and people in the Juniper-Cross Mountain Project area. A detailed field survey has been conducted and further survey work is planned as well as classification of sites, test excavation of some sites at $5,000 each and full excavation or protection of other sites at a cost of $30,000 each. Much of this work has been done by the Laboratory of Public Archeology of Colorado State University under contract with project sponsors. The outline for the cultural resources survey has been approved by the State Historic Preservation Officer. An additional $130,750 is budgeted for a detailed archeological field survey, classification, investigation and photographing.

Some artifacts will be recovered, some finds will be photographed and a detailed report on the data will be established. Results of the studies will be displayed in the Cross Mountain Dam Interpretive Center and/or given to Moffat County for its museum. An additional $11,500 has been budgeted for a detailed paleontology study of trace fossils plus special signing and monitoring of the area. In compliance with state and federal mandates, all of these steps must be taken prior to filling of the reservoirs.

LAND USE

The Juniper-Cross Mountain Project area will be controlled by the Colorado River Water Conservation District and those agencies or concessionaires who may contract with the River District to provide certain services in the project area. The project area generally consists of those lands included in the high water mark of the reservoirs plus additional land up to a 200-foot perimeter around the reservoirs and river channel between them to allow for the protection of the project and provide for recreational and operational facilities. Land use within the project area will be limited to project-related features. The public will have access to the entire project area except for small areas involving power generation equipment, safety or security.

Land use decisions outside the project area are under the control of the Moffat County Commissioners. Presently, lands around the project are zoned agricultural and limited to those uses generally allowed in that zone, primarily residential with minimum five-acre lot sizes and agricultural-related. Any change in that use must go through the formal Moffat County Planning process involving the Moffat County Planning Commission and the Moffat County Commissioners.

MITIGATION

Nearly $4 million has been identified in the project's budget for environmental mitigation measures including the multilevel outlet works on the two dams. Those mitigation measures range from the sighting of transmission lines to avoid a skyline effect and design of transmission structures to avoid electrocution of raptors, to the planting of 5,000 trees and special consideration for the land, plants and animals generally. But the mitigation measures go well beyond. Sensitivity to the land and the environment has been plugged into virtually every feature of the project. This special consideration, whether it is a road design or the use of non glare conductors or the restoration and minimal disturbance of the land through construction, all substantially increase project cost but cannot all be separated from those costs.

The Juniper-Cross Mountain Project's construction force will likely crank up at a time when there will be a projected employment dip in Moffat County as a result of the completion of other projects. Thus, rather than being an impact, the construction force will likely eliminate the impact of a community work force reduction. The same holds true for most of the project's recreation use. While many tourists will come from remote areas spending money in the region and enjoying the project's features, they will likely be dispersed and in a minority. The project will generally serve as a local recreation project, much like a city park or recreation center for people mainly in a three-county area but also beyond.

The Colorado River Water Conservation District will own the dams and reservoirs. As a tax-supported agency, supported in part by Moffat County, the River District does not pay property taxes. Colorado-Ute Electric Association, however, will own the transmission lines going from Juniper-Cross to a Craig switchyard. Colorado-Ute will pay taxes on the transmission lines and those taxes are estimated at more than $200,000 per year in Moffat County based on present levies.

HISTORIC ECHOES

The history of both Dinosaur National Monument and attempts to develop water resources in Northwest Colorado are intertwined. Federal power site reserves and reclamation withdrawals were made for such projects as the Brown's Park Reservoir, Echo Park and Split Mountain reservoirs and Cross Mountain and Juniper reservoirs before paleontologist Earl Douglass discovered an accumulation of petrified dinosaur bones in Northeastern Utah that later became Dinosaur National Monument.

Citizens in the Eastern Utah/Northwestern Colorado area not only strongly supported development of the water projects but also the later expansion of Dinosaur National Monument. While Douglass' find was established as Dinosaur National Monument, an 80-acre tract, by Presidential proclamation in 1915, efforts began in the thirties to expand the Monument.

Citizens of the Craig area particularly pushed for the expansion of Dinosaur to 203,885 acres but always with provision that Echo Park and Split Mountain reservoirs would be constructed. The two sites were outside of the original 80-acre tract but would be included in the expansion.

With the understanding that expansion of the Monument would not preclude water development, the push continued and resulted in a July 14, 1938 proclamation by Franklin Delano Roosevelt expanding Dinosaur National Monument and stipulating that such expansion was subject to provisions of the Federal Water Power Act.

In the late 1940's and early 1950's as efforts to construct Echo Park and Split Mountain reservoirs began to take shape, the organized environmental movement attacked the proposal as a violation of the National Park System.

The efficiency of Echo Park Reservoir, in terms of high power production and minimal evaporation, was pooh-poohed as environmentalists mounted an unrelenting national battle. Part of the attack included the emphasis on optional reservoirs. Environmental organizations quickly adopted the cry that no provision was made for construction of the reservoirs when the Monument was expanded and that there was no need to breach the Monument proper when such optional reservoirs existed as Cross Mountain.

Cross Mountain Reservoir was repeatedly pushed by most groups as the favored, primary option to Echo Park. The Cross Mountain Reservoir of that day was a massive 5.2 million acre-foot reservoir that stretched from Cross Mountain to near Craig and inundated the entire town of Maybell.

The attack was so great that Utah Senator Arthur V. Watkins, a leader in the effort to build the projects, conceded that, regardless of the legal right to construct them and regardless of the ultimate victory in any court battle, the pressure was too great to continue and in 1956 proposals to construct Echo Park and Split Mountain reservoirs were dropped.

On February 14, 1977, the Colorado River Water Conservation District, a 15-county, quasi-municipal entity, was issued a preliminary permit to study the Juniper-Cross Mountain Hydroelectric Project. This project is substantially smaller than the 5.2 million acre-foot Cross Mountain Reservoir of 30 years ago. In total, the project involves some 1.3 million acre-feet of water storage and does not inundate the town of Maybell.

Since the filing of the preliminary permit and the subsequent formal filing of the license application to construct the project, several elements of the organized environmental movement have come forward actively seeking designation of Cross Mountain as a BLM Wilderness Study Area, designation of the Yampa River downstream as a Wild and Scenic River and generally and actively opposing the construction of the project.

A complete and documented history of these events is available on request to the Colorado River Water Conservation District.

CROSS MOUNTAIN

The Bureau of Land Management has designated Cross Mountain as a Wilderness Study Area (WSA) under an inventory process provided for in the 1976 Federal Land Policy and Management Act. In the designation of Cross Mountain, no consideration was given to other resources in the area as required by the Act. Additionally, no consideration was given to power site reserves made more than 70 years ago and some 67 years before the Act was adopted by Congress. Following both the designation and a federal court ruling on another unit, BLM acknowledged that mineral leases predating the 1976 Act, as valid existing rights, are not subject to the non-impairment criteria involved in the wilderness study process. Though not specifically covered by the case, the power site withdrawals represent a similar valid existing right.

Furthermore, in the designation of Cross Mountain as a WSA, a lack of wilderness characteristics and abundance of the imprints of man in the area were ignored. One improved road leads directly to the canyon rim on the south side of the river while another leads well into the designated area on the north side of the river. From all of the mountain but the very top part of that area north of the Yampa River, there is a clear view of U.S. 40 or the Deer Lodge Park Road with noise from that traffic as well as the developed surrounding valleys heard clearly within the unit. The unit is overlaid with numerous grazing permits and stock improvements as well as oil and gas leases. All of this is in violation of the WSA criteria. The top flat part north of the river, though relatively free of the imprints of man, is exposed to the sights and sounds of heavy commercial air traffic as well as some of the noises from below. And, that portion measures less than the 5,000 acres required for a WSA.

Generally, neither the mountain nor its canyon contain the outstanding values required by the 1976 Act. The terrain and vegetation is very similar to that found throughout Southern Wyoming, Eastern Utah and Western Colorado. From a geological standpoint, Cross Mountain Canyon is the same as Black Canyon, Dominguez Canyon, Ruby Canyon, Mee Canyon, Little Dolores Canyon, Dolores Canyon, Hunter Canyon, Garvey Canyon, Big Salt Wash Canyon, West Salt Creek Canyon and Rough Canyon. These are just a few of the canyons in Western Colorado within close proximity to Cross Mountain Canyon.

Other units dominated or influenced by the noise from vehicles or units where freedom of movement is constrained as a result of steep slopes or rugged terrain such as a canyon, have already been eliminated from further consideration as WSAs.

Construction of Cross Mountain Reservoir, as designed, will inundate less than the bottom one-third of the canyon and provide access to a far greater number of people than presently see the canyon from below. From the rims above, the reservoir will not be visible from a point about two feet back from the edge. Any wilderness characteristics that may exist in the unit will continue to exist with construction of the dam.

SALINITY

Salinity increase from the Juniper-Cross Mountain Project due to leaching from the reservoir basin will be very small. While about half of the reservoir basin is on soils derived from the Mancos shale formation, all but 4,400 of these acres are covered with alluvial material which has already had most of the salt removed. In addition, the cold water on the bottom of the reservoir will not readily dissolve gypsum, the primary salt present in Mancos shale. River district consultants, the U.S. Bureau of Reclamation and the U.S. Army Corps of Engineers confirm that they know of no documented situation in which reservoir-leached gypsum has contributed significantly to the salt content of reservoir water or of the water released from the reservoir.

EXISTING RECREATION

For a wide range of reasons, recreation use of the Juniper-Cross Project area as it is today is limited. Different studies have described fishing use of the Yampa River between the bridge west of Craig and Dinosaur National Monument as being limited to about 200 fishermen days per year. Hunting is generally concentrated on the ridges above the project and there is no commercial rafting on the river in the project area.

Because the river through the Juniper Reservoir area is generally considered an undesirable running stretch of river and due to limitations brought about by private land ownership, rafting in the area is limited to some itinerant floating. The Yampa River through Cross Mountain Canyon offers virtually no boating opportunities in that massive boulders create huge waterfalls at high flows and serve as obstructions during low flows.

A group of world-champion kayakers tried and failed to navigate the canyon stretch. There are news accounts of sevral failed attempts to navigate the canyon and most authorities consider it impassable. A group of professional rafters successfully rafted through the canyon about seven years ago and indicated they would never do it again. A long-time area rafting authority indicated that the number of successful attempts to boat through Cross Mountain Canyon would total less than a half-dozen in history.

SELECT SPECIES

Two fish species figure prominently in the Juniper-Cross Project: the Colorado Squawfish and Humpback Chub. Generally, flows from Cross Mountain Reservoir downstream are expected to enhance habitat and spawning for these species as well as several others.

One of the primary causes of diminished population of such fish has been the stocking of other, competing species by state and federal fish and wildlife agencies. U.S. Fish and Wildlife Service listed the two fishes as endangered in 1973 based upon little knowledge, and eight years later began a study of the fish.

With flow releases from Cross Mountain Dam improving habitat downstream and consideration of mitigating features for habitat in the project area, Juniper-Cross Mountain Hydroelectric Project will likely improve the status of these fish as well as other species downstream.

Although the existence of several species of concern in the project area has been cited by some people and organizations, most of those species, such as the Peregrine Falcon, Spineless Cactus and Uinta Basin Hookless Cactus are not anywhere near the project area, according to all published and known reports, recent field investigations and recognized authorities.

The eagle will be affected in the sense of some perches eliminated and hunting grounds modified but several measures have been proposed to mitigate that impact.

Some $1.2 million has been budgeted in the project for terrestrial enhancement and mitigation. Additionally, $2 million has been added to the cost of the project for multi-level outlet works in each dam to control the temperature of reservoir releases for fish. However, if, prior to construction, it is found that multi-level outlet works are not necessary, they will not be included.

One botanical species of concern, the Penstemon Yampaensis, may be affected by the project. There are several populations of the Penstemon in Moffat County; two are in the project area. Mitigating measures may include transplanting in the general area, making arrangements for nurturing in botanical gardens and seed collection for deposit in a national seed bank.

Impact on other species of concern is either nominal or easily mitigated.

EXISTING RECREATION * * * SELECT SPECIES

FUTURE RECREATION* * * LAND ACQUISITION

POWER VALUES * * * * * * * * * * WILD & SCENIC

FUTURE RECREATION

Recreation needs of Northwest Colorado continue to mount and go unfulfilled. The 1981 State Comprehensive Outdoor Recreation Plan (SCORP) cites Region 11, which includes the four Northwest Colorado counties, as the fastest growing region in the state for the past few and next few years. The plan cited a high need/significance for the region in such activities as picnicking, swimming, camping, lake boating, fishing and nature study.

The SCORP generally followed the results of a 1980 Moffat County Recreation survey showing those activities or features that residents of the county would like to enjoy.

The Juniper-Cross Mountain Project will ultimately accommodate 500,000 recreation days per year. Each reservoir will have one major boat landing, one boat ramp and a 50-boat marina. A self-guiding, interpretive center will be located near Cross Mountain Dam. Camping sites and picnic areas will be constructed at the outset and gradually increased on the basis of actual demand. Special provision is made in the recreation plan to accommodate those people who wish to recreate in a particular pace or style: there will be four-wheel drive vehicle areas, hiking trails, areas in which speed boating will be allowed, and areas in which speed boating will be prohibited and casual boating encouraged. Special attention has been paid in the recreation plan to provide access to beautiful areas that can not now be reached by most people.

The project sponsors anticipate spending $300,000 to develop fisheries in the reservoir which will likely include both cold and warm water fisheries, taking advantage of reservoir stratification and offering a variety of fishing opportunities.

It is anticipated that not only will hunting be allowed in the project area, but that hunting, at least with regard to water fowl, will increase as a result of ponds or wetland areas that will likely be established in conjunction with the main reservoirs.

Like most water storage projects, Juniper-Cross Mountain will smooth out both peak and low flows, spreading water availability out across different seasons of the year and different years. For the 15,000 to 20,000 rafting days downstream on the Yampa River in Dinosaur National Monument and below, that will mean lower peak flows as well as higher low flows. The more moderate flows from Juniper-Cross will allow for an extension of the rafting season in normal years and most likely will be what enables any rafting season at all in dry years.

First phase recreation features will be constructed along with the project at a cost of $1,250,000 and will accommodate 150,000 recreation days per year. A majority of the use will likely come from residents of the region and future residents related to energy development. An area resident may fish or boat at the reservoirs 40 times a year, which would count as 40 recreation days, while a Denver couple may spend a week at the reservoir, which would account for 14 recreation days.

Beside the service to area residents in the form of recreation, the project will provide several million dollars per year in economic benefit to the region through tourism.

LAND ACQUISITION

About half of the land required for the Juniper-Cross Mountain Project and related features is privately owned. The River District has met with and responded to questions from landowners in the project area. Soon after the project is licensed, the River District will commence negotiations with landowners. The River District has the power of eminent domain under both state statute and the Federal Power Act and is required by law to pay just compensation to property owners for land taken for the project or property damaged as a result of the project. In the event negotiations cannot be settled to mutual satisfaction, just compensation will be set by court appointed commission or a jury of six.

POWER VALUES

No comparison can be made between a coal-fired base load power plant and a hydroelectric power plant – the two serve completely different but complementary functions. Hydroelectric power is the most feasible form of generating "peak" power on a commercial basis. "Peaking" is that power needed on immediate demand when most consumers or other power users cause a sudden increase on the power system. As an example, there is a generally steady power demand in some areas through the day until evening, when many people go home from work and turn on TV sets, appliances, lights and so on. Most power systems have such irregularities; irregularities or peak demand periods which occur at certain times of the day and during certain seasons of the year.

Coal-fired power plants, such as those operated by Colorado-Ute in Craig and Hayden, are an extremely effective form of providing baseload power – serving the constant demand. But, they are slow to respond to sudden changes in system demand. Hydroelectric power, on the other hand, is the most effective power source available for meeting those sudden changes. Water in a reservoir functions as a battery and involves no waste or lost efficiency. When a sudden demand strikes the system, the water can be released through turbines generating peak power for as long as that peak is needed and generating it immediately.

The total power production of Juniper-Cross Mountain is significant in that it can fulfill all energy needs except heating for some 40,000 homes while displacing 600,000 barrels of foreign oil per year. It is five times greater than Glenwood Canyon's Shoshone Plant and 18% greater than the Cameo Steam plant at DeBeque Canyon. However, the most significant feature of power production from Juniper-Cross is the production of "peak" power. More than half of the 350 million kilowatt hours of clean, renewable power that will be produced by Juniper-Cross will be peak power. By most standards, peaking power is twice as valuable as baseload power.

In addition to providing peaking power, Juniper-Cross may be used to generate power in the event a major baseload plant is down for repairs or maintenance. This is a part of the effort aimed at trying to avoid interruption of service to the consumer regardless of contingencies. Cross Mountain will generate some peaking power but will primarily generate baseload power in its function of reregulating peak water releases from Juniper.

It is the value of the power and revenue from its sale that will pay for millions of dollars in fish and wildlife mitigation and recreation features – that will pay for the project entirely. There are no state or federal monies involved in Juniper-Cross.

WILD & SCENIC

The National Park Service has recommended designation of 91 miles of the Green River and 47 miles of the Yampa River in Dinosaur National Monument for inclusion in the National Wild and Scenic River System. Although the Park Service's recommendation came from a draft Environmental Impact Statement dated April 30, 1979, the determination was made in 1976, contrary to a Congressional Act that requires conclusion of a study in order to make a determination.

In a Bureau of Outdoor Recreation letter dated August 13, 1976, some three years before the draft was published, it was stated that "The study team for the Yampa and Green Wild and Scenic Rivers Study has determined that the Yampa River within Dinosaur National Monument qualifies as a Wild River Area according to the criteria specified in the Wild & Scenic River Act, P.L. 90-542. The outstandingly remarkable qualities identified in and along this segment of the Yampa are its scenic, recreational, geologic and fish values." Following that conclusion, the study was made, apparently to substantiate the result arrived at three years earlier.

As to recreational values, the Park Service currently limits the number of rafting days to about 20,000 per year as compared with the anticipated use of 500,000 recreation days per year in Juniper-Cross Mountain reservoirs. Several biologists find the advantages of a steady flow from a reservoir to be far more advantageous to certain fishes than the natural extremes of flood and drought. Construction of Juniper-Cross Mountain on the Yampa River would not change the scenic or geologic features downstream in Dinosaur. Indeed, the same National Park Service has recommended for inclusion in the system as a Scenic River, the stretch controlled by and immediately below Flaming Gorge Dam.

The river stretches proposed for designation are inside Dinosaur National Monument, where the National Park Service already has absolute control. Thus, the significance of Wild and Scenic designation is not the impact on the stretch of river in question but the impact upstream. An opinion by the Attorney General of Colorado in 1976 indicated that such designation precludes any form of development that may diminish the scenic, recreational and fish and wildlife values in the river portion under consideration or so designated.

Additionally, the Act makes provision for condemnation of water rights in order to insure the wild and scenic values described. Thus, while National Park Service authority is presently limited in Northwest Colorado to the boundaries of Dinosaur National Monument, designation of the Yampa River in Dinosaur as a Wild River would extend National Park Service authority through private property and up to the headwaters of the Yampa.

NOTES:

This booklet is intended as a discussion of various issues and not as a complete project summary. Those seeking more information about the project should contact:

Colorado River Water Conservation District
P.O. Box 1120
Glenwood Springs, Colorado 81602
303/945-8522

Copeia, 1983(1), pp. 37–48

Taxonomic Relationships of the Zuni Mountain Sucker, *Catostomus discobolus yarrowi*

G. R. Smith, John G. Hall, Richard K. Koehn and David J. Innes

Catostomus discobolus yarrowi **of the Little Colorado River drainage in New Mexico and Arizona is variable, with populations morphologially and biochemically intermediate between *C. discobolus* of the Colorado drainage and *C. plebeius* of the Rio Grande drainage. Specimens of *C. yarrowi* from the headwaters of the Little Colorado in the Zuni Mountains, New Mexico, are especially similar to populations of *C. plebeius* from just across the continental divide. Downstream populations are more like *C. discobolus*. Morphological and biochemical characters show slightly different trends among samples, but the patterns are consistent with the hypothesis that a late Pleistocene stream capture resulted in introgression of *C. plebeius* characters into *C. discobolus*.**

IN 1874, E. D. Cope described "*Minomus jarrovii*" from the Zuni River headwaters of the Little Colorado River drainage in New Mexico, based on specimens with 9 dorsal fin rays and the lower jaw "with acute cartilaginous edge, regularly convex forwards." The types (USNM 15783) were collected by H. W. Henshaw in 1873. [Cope gave the type locality as Provo, Utah, but Cope and Yarrow (1875) corrected it to the Zuni River, New Mexico.] Fowler (1913) referred to specimens from the same drainage, at Fort Wingate and Nutria, New Mexico, as *Pantosteus plebeius,* a species with the above characters, living in the Rio Grande drainage. The populations were rediscovered in other Zuni tributaries by W. J. Koster: the Rio Pescado in 1948 and Nutria Creek in 1960.

Smith (1966) showed that the Zuni River suckers (Fig. 1a, d) were similar to *C. discobolus* Cope (1872) of the Colorado drainage (Fig. 1c) in the number of gill rakers, but were similar to *C. plebeius* Baird and Girard (1854) of the Rio Grande drainage (Fig. 1b) in numbers of vertebrae and dorsal rays, jaw size and shape, and pigment. The mosaic of *C. plebeius* and *C. discobolus* characters in the Zuni and other Little Colorado River populations were regarded to be the result of an ancient stream capture from the Rio Grande to the Zuni, and introgressive hybridization. Smith (1966) assigned the Zuni populations to *C. discobolus* because they possessed the diagnostic gill raker numbers of that species. Although the Zuni populations were interpreted as descendants of intergrades, the

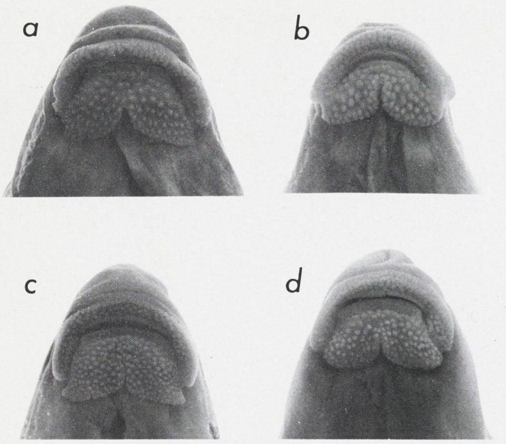


Fig. 1. Shapes of jaws and lips of a) *C. d. yarrowi* (×1.4), Nutria Cr.; b) *C. plebeius* (×2), Cottonwood Cr.; c) *C. d. discobolus* (×1.4), Whiskey Cr.; d) *C. d. yarrowi* (×1.4), Rio Pescado.

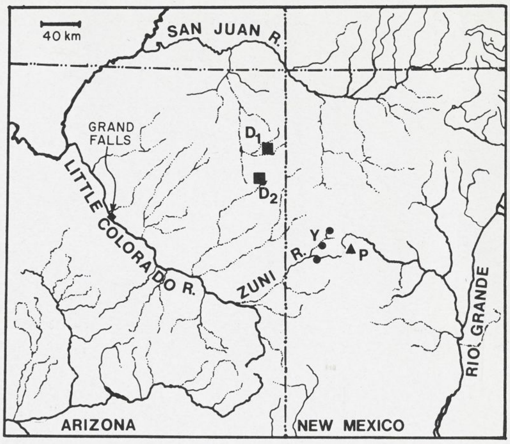


Fig. 2. Sample locations in the Little Colorado drainage and other drainages. D_1 = Whiskey Creek, *C. discobolus*; D_2 = Kin Li Chee, *C. d. yarrowi*; Y = Zuni drainage, *C. d. yarrowi*; P = Wells Spring, *C. plebius.*

much reduced overlap in the number of gill rakers (see below) was used to justify failure to synonymize *C. plebeius* and *C. discobolus.* The contention that the Zuni Mountain sucker populations are natural, not introduced, is based on the presence of the phenotype in 1873, before extensive fish transplants were practiced in the West.

In 1978, specimens were collected in the Zuni River drainage in order to test the hypothesized stream capture and intergradation. Reference samples of *C. discobolus* and *C. plebeius* were also taken. Morphological and biochemical characters are used to estimate the nature of the similarity of the Zuni populations to *C. plebeius* and *C. discobolus.*

Several alternative hypotheses must be considered. They are not all mutually exclusive. It is possible that the Zuni populations are 1) intergrades resulting from a stream capture, 2) an intermediate part of a polytypic species including *C. plebeius* and *C. discobolus,* 3) the expression of ecophenotypic or locally selected character states with no historical interpretability or 4) a distinct species. Hypothesis (1) was suggested by Smith (1966) based on morphological data analyzed one character at a time. It predicts that the biochemical characters should also show a mosaic of *C. plebeius* and *C. discobolus* states, with *C. plebeius* states predominant nearest the site of the supposed capture and *C. discobolus* states predominant downstream. Lack of *C. plebeius* character states, or a different pattern of state frequencies in the Zuni suckers would discredit this hypothesis. Possibility (2)—one polytypic species—is not inconsistent with (1) or (3), but involves a different taxonomic interpretation. It is favored if species-diagnostic distinctions between *C. plebeius* and *C. discobolus* cannot be demonstrated. Possibility (3), that the critical characters (jaws, lips, gill rakers, numbers of fin rays and scales) are expressions of ecophenotypic effects or results of local selection, can be examined in the context of observed variation of *C. plebeius* and *C. discobolus* in similar habitats elsewhere. (4) If the Zuni suckers were to display unique character states making them diagnostically separable from *C. plebeius* and *C. discobolus,* they would warrant specific recognition. Subspecies recognition will be supported by evidence of unique combinations of character states showing overlap with those of one of the species. This interpretation is not inconsistent with (1), (2) or (3).

Methods

Tributaries in the Little Colorado River drainage were surveyed to determine the distribution and abundance of mountain suckers (Figs. 2, 3). Former habitats throughout the drainage (Smith, 1966:89) were sampled by electrofishing, including the Little Colorado in Navajo and Apache counties (three localities,

9. The Colorado River system

J. A. Stanford & J. V. Ward

Introduction

The American Southwest has long captured the awe of wayfarers, struck by the apparent hostility of its eroded wastelands. The area contains the Mohave and Sonoran deserts and on centre stage is the Colorado River, whose silt-laden waters have eroded magnificent canyons in lowland regions of the United States and northern Mexico (Fig. 1; Crampton 1964). Fed by snowmelt from the southern Rocky Mountains, the Colorado drains 1/12th of the United States, although its annual discharge is relatively low. The river carved the Grand Canyon, the largest gorge in the world, and its waters have spawned the economic development of the Southwest (Williams 1951; Fradkin 1981).

In the late 1600s the first Spanish explorers ventured from Mexico into the Colorado Basin *via* the San Pedro River, but were sobered by the hostile environment. Along the middle Gila River they found a sophisticated network of canals that had irrigated prehistoric crops. The only remnants of these early river regulators were wandering bands of Apache and Piman Indians whose ancestors, the Hohokam, once fished the rivers for giant minnows and farmed the desert with water diverted from the Gila. The Hohokam and other advanced, prehistoric cultures of the American Southwest may have failed during a dry period, when the rivers did not supply enough irrigation water (Euler *et al.* 1979). The Spaniards returned to Mexico; development awaited hardy Mormon pioneers 300 years later.

In the late 1800s settlers began in earnest to divert Colorado waters into the deserts. By 1903, water was flowing *via* new canals into the valleys of southern California. A Federal reclamation law allowed construction of further diversions and storages, and in 1910 Roosevelt Reservoir was constructed on the Gila River. Diversion projects began also in the Colorado headwaters. In 1935 the construction of Hoover Dam to form Lake Mead (Fig. 1) harnessed spring floods from headwater snowmelt. The economic benefits of Lake Mead are countered by the realisation that the riverine ecosystem evolved in harmony

The Ecology of River Systems, edited by B. R. Davies & K. F. Walker

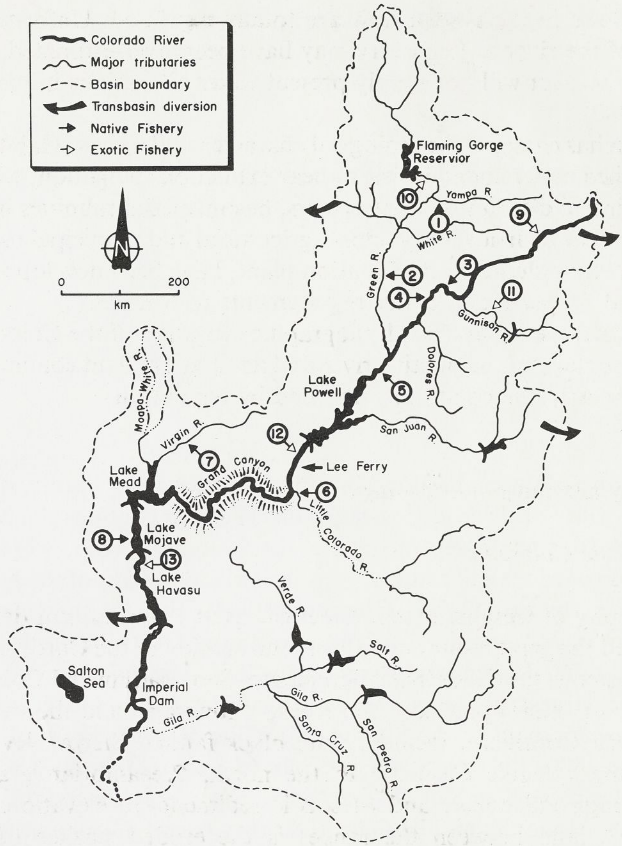


Figure 1. The Colorado Basin. Intermittent reaches are shown as broken lines. Important native (solid triangle) and exotic (open triangle) fisheries also are marked.

with the spring freshet. The floodwaters renewed the vast desert marshes, cued spawning of riverine fish and encouraged the growth of riparian plants. But the fate of the river was sealed; it remained only for flows to be allocated among the basin states.

After years of argument (cf. Hundley 1975), the Colorado was legally divided into Upper (Wyoming, Colorado and Utah) and Lower Basins (Arizona, California & New Mexico) at Lee Ferry, above the Grand Canyon (Fig. 1). Allowances for each state were based on the estimated average annual flow at Lee Ferry. A federal scheme of reservoirs and diversion canals facilitated delivery of water shares to each state, leaving only a small amount for Mexico. The major works have now been built, except for canals now under construction to divert water from below Lake Mead into central Arizona. Except in small tributaries, flows in the system now are totally regulated. Unfortunately, the virgin flow of the river at Lee Ferry may have been over-estimated, and many believe that the river will not supply present water allocations in the long term (Spofford 1980).

Regulation has changed the ecological character of the river. Habitat destruction has pushed many endemic fish to near extinction. Irrigation, with evaporation and mineral dissolution in reservoirs, has increased salinities in the lower reaches to levels which adversely affect agricultural and municipal uses. Salinity control projects, including a desalination plant, have been developed to reduce salt loads and deliver treaty water requirements to Mexico.

In this chapter we review the physiographic evolution of the Colorado River, describe the ecology of the pristine river and its riparian plant communities, and contrast these with the conditions imposed by regulation.

Physiography and fluvial morphology

Evolution of the Colorado

The topography of western North America results from crustal deformations which uplifted the great mountain ranges, and erosion of the Cordillera by three great river systems: the Columbia, Sacramento–San Joaquin and Colorado (Fig. 2). Mesozoic orogenies produced the Rocky Mountains and the varied ranges of the western Cordillera, including the block-faulted Sierra Nevada to the south and the volcanic Cascades to the north. Precambrian granites were uplifted through Palaeozoic and Mesozoic sediments to elevations exceeding 4000 m. Most land between the ranges is the eroded surface of these old sedimentary formations. During this process the interior Cordillera subsided, and erosion sculpted the plateaus and plains of the Great Basin. Another portion, the Colorado Plateau, was uplifted to its present elevation of 1500–2500 m (tilted downward E–W), with little of the compression that folded and faulted the sediments of the Great Basin and the flanks of the Rockies (Clark & Stearn 1960).

Drainage from the developing Cordillera was influenced by the rain-shadow effect of the western ranges on weather systems moving from the Pacific Ocean; this accounts for the deserts between 36–39°N (Fig. 2). Historically, the Great Basin has received little precipitation compared to the mountains on either side, although latitudinal shifts in climate may have produced vegetational changes in the last 24 000 years (Cole 1982). Drainage from the western side of the southern Rockies proceeded across the Colorado Plateau to the southern perimeter of the Great Basin, where little more water was generated. The Colorado River assumed its present position by the Pliocene, if not earlier (King 1958, 1959).

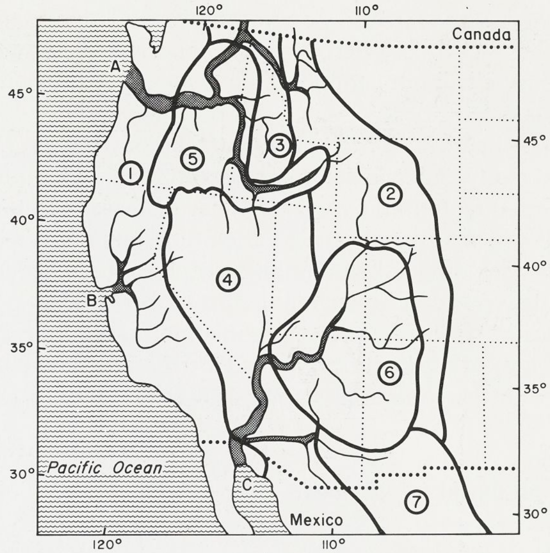


Figure 2. Physiographic provinces of the North American Cordillera: (1) western ranges, (2) Rocky Mountains, (3) interior ranges, (4) basin and range (Great Basin), (5) Columbia Plateau, (6) Colorado Plateau and (7) Mexican Plateau. Major river systems draining the Cordillera are (A) the Columbia, (B) the Sacramento-San Joaquin and (C) the Colorado.

With strong headwater flows and a 2500 m change in elevation, the river cut deep canyons through the rising plateau, exposing sequentially the geologic history of the Southwest. In Black Canyon on the Gunnison River (Stanford & Ward 1984) and Grand Canyon on the mainstem (Plate 1), the river reached the Precambrian basement, so that nearly all formations underlying the basin are visible on the canyon walls (Fig. 3). Historically, the rate of basin-wide erosion above the Grand Canyon has been *c.* 17 cm per 1000 years (Bishop & Porcella 1980).

Near the end of mountain building in the Tertiary, the middle of the Great Basin arched upward from *c.* 300 m to more than 1500 m above sea level. Weathering yielded the Basin and Range Province, a series of ranges, plateaux and buttes (Fig. 2). Drainage from these ranges and from the Sierra Nevada and Rocky Mountains accumulated in pluvial lakes on the west (Lake Lahontan) and east (Lake Bonneville) of the Great Basin. Lake Bonneville (Fig. 4) reached maximum development about 28 000 years ago, when it was more than 300 m deep and 50 000 km^2 in area. Lake levels oscillated with the climate, and began to recede 10–15 000 years ago. Desert or semi-desert lands claimed the lowlands soon after the Pleistocene, and the lakes were reduced to saline remnants: thus

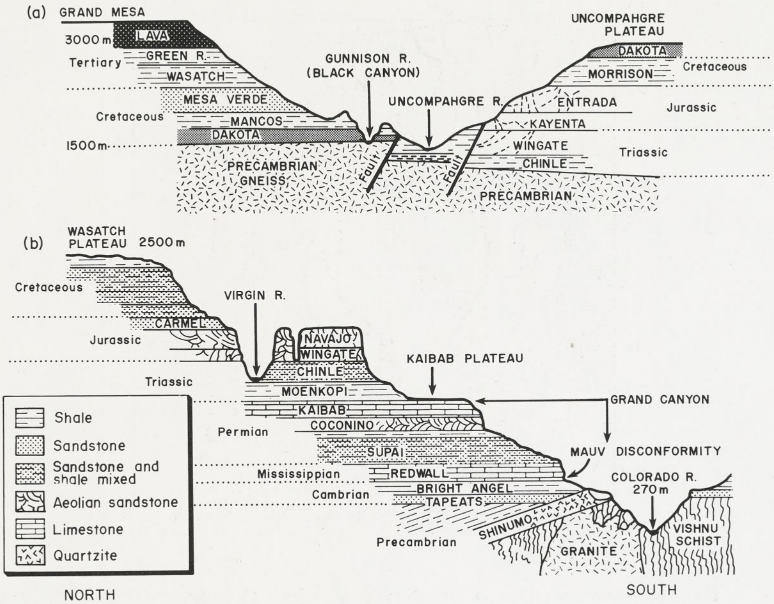


Figure 3. Geologic formations of the Colorado River Basin: (a) structures in a N–S section of the lower Gunnison Valley, Colorado (based on Chronic 1980; Stanford & Ward unpublished), (b) major exposures in the N–S section from Wasatch Plateau, Utah, to the bottom of the Grand Canyon (after Strahler 1963).

Pyramid Lake in Nevada and Great Salt Lake in Utah (Hubbs & Miller 1948; Clark & Stearn 1960).

Lake Bonneville was never connected to the Colorado system, but a series of smaller pluvial lakes drained *via* the White River system (Moapa-White River and Meadow Valley Wash: Fig. 1). These flowed south into a large lake, Hualapai, on the Colorado at the mouth of the Grand Canyon. Other pluvial lakes were present on the Gila River and in the Salton Depression near the river mouth (Fig. 4).

A unique fauna evolved in the Pleistocene Colorado. Although the fossil record is not completely understood, the Pliocene fish fauna diversified in the mesic Pleistocene environment. For example, a unique assemblage of minnows (Cyprinidae) and suckers (Catostomidae) evolved in the mainstem while other minnows and trout (Salmonidae) diversified in the headwaters. Mainly subspecific differentiation occurred after the Pleistocene, as desertification exerted strong selective pressures on populations isolated in the disrupted White River and parts of the Gila River (Stanford & Ward 1986a). About 8000 years ago the natural character of the river was determined, and remained so until Lake Mead was formed in 1935.

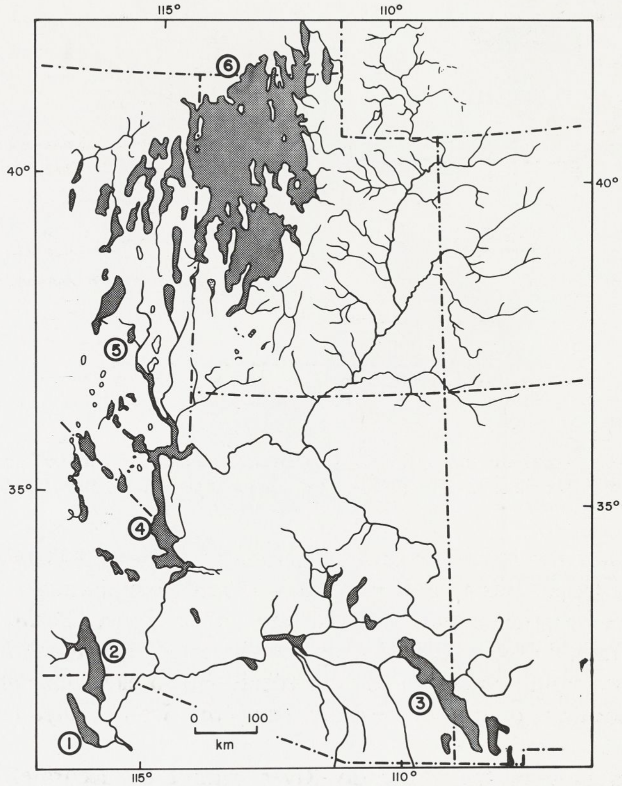


Figure 4. The maximum extent of late Pleistocene lakes and known fluvial connections to the Colorado River: (1) Lake Pattie, (2) Lake LeConte, (3) Lake Morrison, (4) Lake Hualapai, (5) Pluvial White River system and (6) Lake Bonneville (after Smith 1978; Miller 1981).

Morphology and discharge

The Colorado originates in a subalpine meadow (3105 m) in Colorado's Rocky Mountain National Park, and from there flows 2320 km to the Gulf of California. With the Green River, which originates at Peak Lake in the Wind River Mountains of Wyoming, the Colorado is more than 2700 km in length (Fig. 1). Major sub-basins include the Gila (145 000 km^2), Green (115 000 km^2), Upper Mainstem (above the Green confluence; 67 000 km^2), Little Colorado (67 000 km^2), San Juan (66 800 km^2) and Virgin (28 500 km^2). The total basin area within the United States is 629 111 km^2 (U.S. Geological Survey data), with another 8600 km^2 forming the delta in Mexico (Sykes 1937).

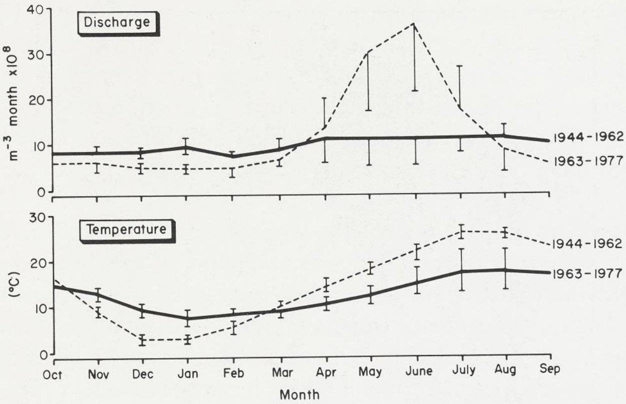


Figure 5. Monthly means and ranges (bars) of discharge and temperature in the Colorado River at Lee Ferry before (1944–62) and after (1963–77) impoundment of Lake Powell (after Paulson & Baker 1981).

All the major tributaries originate in mountains above 3000 m. The headwaters of the Upper Basin, with more than 130 cm precipitation annually, are more mesic environments than the headwaters of the Lower Basin. More than 40% of the annual flow is derived from the Upper Mainstem sub-basin (Irons *et al.* 1965). Precipitation decreases dramatically below elevations of 1500 m (*c.* 70% of the basin), and much of the desert below the Grand Canyon receives less than 15 cm annually.

The virgin flow of the Colorado River cannot be accurately estimated because the various dams and diversions pre-date discharge measurements near the river mouth. However, the average virgin flow at Lee Ferry is estimated at 18.35 $km^3 a^{-1}$ for 1914–65 (Bishop & Porcella 1980). The annual hydrograph peaked in spring, in response to snowmelt (Fig. 5), generating flows of 2400–5600 $m^3 s^{-1}$ in the Grand Canyon (Carothers & Minckley 1981). Most virgin flow came from the Upper Basin, but winter storms often flooded the lower river with silt-laden waters from the Little Colorado and Gila rivers. Maximum runoff in the Gila Basin usually occurred in winter, with flows up to 1500 $m^3 s^{-1}$ (Sykes 1937). Based on U.S. Geological Survey data, the pre-regulation average annual flow at the Colorado Delta was *c.* 19.0 $km^3 a^{-1}$ (602 $m^3 s^{-1}$). The highest recorded flow is 7100 $m^3 s^{-1}$ on 22 January 1916, but flows greater than 10 000 $m^3 s^{-1}$ probably have occurred in the last 200 years (Dill 1944). Lowest flows occurred in mid-late summer; the minimum for 1902–34 was less than 10 $m^3 s^{-1}$ on 25–27 August 1934. The annual unit-area discharge for the entire basin (637 711 km^2) is 29 800 $m^3 km^{-2}$, indicating one of the driest river basins in the world.

The sediments of the Colorado Plateau are highly erodible, so that slight flow increases accelerate sediment loading in all sub-basins. Sediment movement through the Grand Canyon before impoundment averaged about 374 t d^{-1}, and much higher rates occurred in floods. Spring runoff in 1927 generated a peak flow of 3538 $m^3 s^{-1}$, carrying 27 164 t d^{-1} through the canyon (Dolan *et al.* 1974). Sediment deposition on the delta (Plate 1) varied from a few tonnes daily to more than 1000 tonnes each *second* during floods (Sykes 1937). The virgin Colorado was the greatest conveyor of sediments of any river in the world (Dill 1944).

Present flows are unlike those of the virgin river. Dams and diversions have virtually de-watered the lower Gila River and many of the channels on the delta (Figs 1 & 3), where flows now occur only in response to infrequent, localised rainstorms. The only significant free-flowing tributaries in the entire basin now are the Little Colorado and White rivers. In the Upper Basin more than 117 reservoirs of capacity greater than 1.0 km^3 have been built or are under construction, and there are proposals for others on the Yampa, White and Gunnison rivers. The total usable storage in the Upper Basin is more than 36 km^3 (Bishop & Porcella 1980), or twice the annual virgin flow at Lee Ferry. In addition, nearly 1 km^3 of water annually is exported from the Upper Basin by more than 40 trans-basin diversions (e.g. Fig. 1). Irons *et al.* (1965) reported that 29% of the water reaching Lake Powell was from upstream storage reservoirs, but that percentage now undoubtedly is much higher. Elsewhere, flows are almost totally controlled by reservoirs. The one reach retaining a near pre-regulation pattern is that above Lake Powell, including the lower Green and mainstem Colorado rivers to near the confluence with the Gunnison River (Fig. 1).

Regulation has had profound effects on flow and sedimentation between Lakes Powell and Mead. Flows from Lake Powell are 130–764 $m^3 s^{-1}$ year-round, thus eliminating the annual freshet (Fig. 5). Sediments are retained in Lake Powell, except those discharged by the Little Colorado River and other sideflows, and the median suspended sediment concentration in the Grand Canyon has been reduced by a factor of 3.5 (Dolan *et al.* 1974; Fig. 6).

Fluvial processes likewise have been affected. Before regulation, alluvial rubble from side-flows formed long, sandy bottom pools separated by short, steep rapids. Dolan *et al.* (1978) showed that side-flows enter along faults or geologically unstable points, where there is often major downcutting by the main river, creating the rapids. Debris-laden floods from side-flows also built sand terraces near the high-water mark, and formed extensive channels and backwaters wherever the floodplain permitted. Post-regulation flows have stabilised the river bottom (Simons 1979; Stanford & Ward 1984; Plate 1), and lack force to move much of the side-flow debris; hence the rapids are growing in length and are more turbulent. Sand bars and terraces are no longer reworked by flood waters, nor are many of the flood channels re-watered.

Thus, the regulated channels of the Colorado system are stabilised by constant (once variable), clearwater (once silt-laden) flows (Dolan *et al.* 1974, 1977;

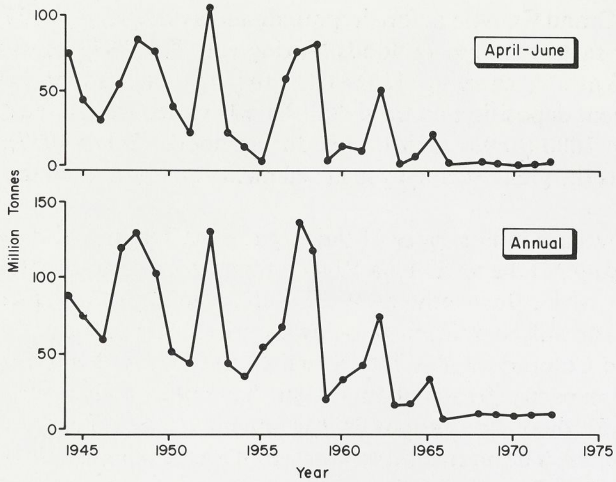


Figure 6. Mean suspended solids loads annually and during spring runoff (April–June) in the Colorado River at Lee Ferry. Lake Powell was impounded in 1963 (after Paulson & Baker 1981).

Carothers & Minckley 1981; Stanford & Ward 1983, 1984). The delta receives essentially no flow from the mainstream and Gila River, due to diversions. Today the delta, once a maze of channels (Plate 1), resembles the surrounding desert.

The Salton Sea

The Colorado Delta is formed as a "T", with arms extending 320 km south from near the Salton Sea to the Gulf of California, and base near the Gila River confluence (Fig. 1). During the Pleistocene, a late Tertiary cryptodepression, the Salton Sink, filled with water to form Lake LeConte (Fig. 4). Subsequent deposition may have accelerated subsidence of the delta, and the river periodically may have flowed into the sink (Sykes 1937; Hubbs & Miller 1948).

Explorers in 1853 found the Salton Sink (Imperial Valley) dry, with the valley floor 83 m below sea level. Between 1900–04 the valley was connected to the Colorado River *via* irrigation canals. In January 1905 flood waters from the Colorado broke through the canal gates, and by late summer virtually the entire river was flowing into the "Salton Sea". The inflow created a lake of 1060 km^2 area and 26 m depth (Sykes 1937), and the river was not returned to the gulf until dike construction in February 1907. Since then diversions have been controlled, but the irrigated lands have expanded to more than 2000 km^2. Imperial Valley now is the largest expanse of irrigated agriculture in the Western Hemisphere (Pillsbury 1981), and uses most of the remaining river flow *via* diversions at Imperial Dam (Fig. 1).

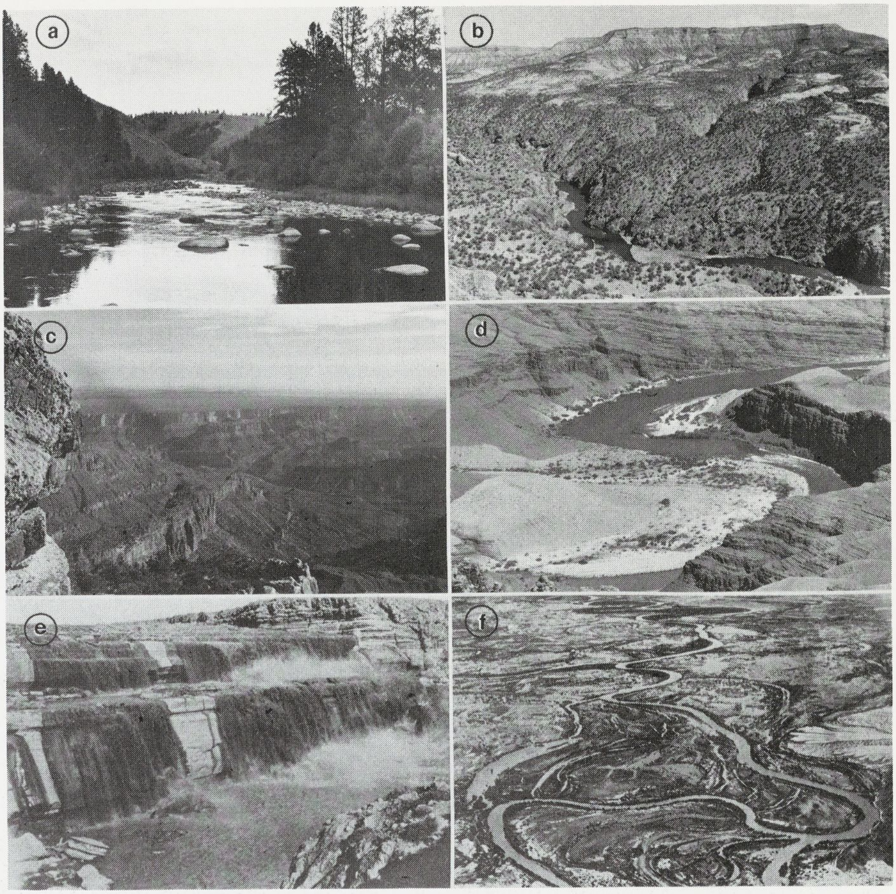


Plate 1. The Colorado River system: (a) the Colorado River at a regulated headwater location below Granby Reservoir (photo JVW), (b) Lower Black Canyon of the Gunnison River, showing Precambrian basement near the river and Mesozoic sediments on the uplands (JAS), (c) Grand Canyon of the Colorado River from the North Rim (JAS), (d) Colorado River in the Grand Canyon (JVW), (e) turbid flood waters of the Little Colorado River at Grand Falls (Sykes 1937), and (f) the Colorado Delta in 1932 (Sykes 1937).

In 1907 the salinity of the Salton Sea was *c.* 3600 mg l^{-1}; it has since increased by an order of magnitude due to evaporation and irrigation runoff. The bottom waters develop seasonal anoxia, and surface temperatures may exceed 35°C. Blue–green algae (e.g. *Phormidium*) dominate the phytoplankton, and brackish-water zooplankters (e.g. *Brachionus plicatilis*) are food for various introduced fish (Walker 1961). Massive fish kills occur each year from algal toxins and chemicals in agricultural and urban runoff (Kim 1973).

River limnology

Temperature

Before regulation, desert reaches of the Colorado in winter rarely dropped below 5–10°C, and summer temperatures did not exceed *c.* 30°C despite air temperatures sometimes above 40°C. Backwaters and marshes, however, often reached 35°C (Deacon & Minckley 1974). Seasonal temperatures in the headwaters range from 0°C to 15–20°C (cf. Deacon & Minckley 1974; Stanford & Ward 1983).

Thermal patterns have been changed by flow regulation, and the mean mainstream temperature has decreased by 10–15C° (e.g. below Lake Powell; Fig. 5). Regulated reaches are characterised by summer-cool, winter-warm conditions (Ward & Stanford 1979). On the Gunnison River water from the hypolimnion of a headwater impoundment (3500 m) prevents the downstream river from freezing, even though air temperatures may be below −30°C for extended periods (Stanford & Ward 1983).

Chemistry

Dissolved solids loads reflect the geology of the various sub-basins. In the Upper Basin, the Mancos Formation (Fig. 3b) is extensively drained. Mancos shales are predominantly gypsum, as are Mesozoic shales elsewhere in the drainage (Laronne & Schumm 1982). Limestones are locally important, particularly in the Grand Canyon (Fig. 3b). Thus Ca^{2+}, $SO_4^=$ and HCO_3^- dominate the composition of Colorado River water. Sulphate consitutes over half of the Total Dissolved Solids (TDS) in the river at the delta. TDS loads increase 2–4 fold as streams flow into the sedimentary formations. In the Gunnison River, average $SO_4^=$ concentrations increase from less than 10 mg l^{-1} in the headwaters (3000 m) to more than 250 mg l^{-1} at the Colorado River (1400 m), primarily due to drainage from the Mancos Formation (Stanford & Ward 1983).

Some reaches drain NaCl formations. The Paradox Valley of the Dolores River, where salt encrusts the river bank, is a textbook example of "salt dome" formation (cf. Clark & Stearn 1960). Even so, Ca^{2+} and $SO_4^=$ dominate at the Dolores–Colorado confluence.

The Little Colorado River is the only major tributary contributing mainly Na^+ and Cl^-, due mostly to high-discharge springs near the confluence. Salt loads also originate from similar springs throughout the Upper Basin (United States Dept Interior 1981).

Various springbrooks in the Grand Canyon issue from the Redwall Formation (Fig. 3b), an impure dolomitic limestone. The water is saturated with calcium and magnesium carbonates (Kubly & Cole 1979), and intricate travertine formations have developed in turbulent areas.

As a consequence of dissolution of gypsum and limestone, the TDS load at the delta before regulation was about 380 mg l^{-1}. Present values exceed 825 mg l^{-1} (U.S. Bureau of Reclamation data) due to: (a) dissolution *via* irrigation and impoundment, (b) diversions of low salinity headwaters, (c) flow depletion *via* evapotranspiration on irrigated land and (d) concentration *via* reservoir evaporation (cf. Pillsbury 1981). Intrabasin diversions now under construction (e.g. the Central Arizona Project) could deplete flows in the lower river by 2.5 km^3, increasing TDS to 1150 mg l^{-1} or more (U.S. Bureau of Reclamation data). Effluents from mines under development in the Upper Basin shales also may be high in TDS (cf. Turk 1982).

In contrast, TDS values in the river below Lake Mead have decreased since 1972. This has been dismissed as a transient phenomenon related to flow or perhaps less dissolution within the basins of Lakes Mead and Powell, but a more general explanation may come from analysis of the impact of mainstem reservoirs on downstream TDS (Paulson & Baker 1983). Stanford & Ward (1984) showed that deep, mainstream reservoirs on the Gunnison River reduce downstream TDS mainly by precipitation of $SO_4^{=}$, and that nitrate levels increase from mineralisation in bottom waters. The reservoirs also limit the seasonal amplitude of ion strength by impounding floods which once diluted the natural river.

The chemistry of the river below Lake Powell is likewise determined by limnological processes in the reservoir, as 97.7% of the flow reaching Lee Ferry is from the lake. TDS values have not been appreciably altered by the lake's formation, although ionic proportions have changed (Table 1). Net losses of Ca^{2+} and HCO_3^- *via* precipitation are offset by evaporation and gypsum dissolution. As the reservoir approaches steady-state with respect to its inherited salt burden (i.e. gypsum dissolution should decrease with time, while $CaCO_3$ precipitation continues unabated), TDS in the river downstream should decrease (Gloss *et al.* 1981). Lake Mead evidently is at or near steady state, explaining the decreased TDS values (Paulson & Baker 1983).

Ecological interactions

Reservoir circulation, trophic status, morphometry and the timing and depth of releases are the primary determinants of tailwater ecology. Stream ecosystem processes (e.g. nutrient spiralling, temperature–flow relationships) progressively ameliorate the tailwater effects with distance downstream (Ward & Stanford 1983; Stanford & Ward 1984). Unregulated side-flows may restore natural conditions in regulated streams if the tributary discharge approaches that of the receiving stream (cf. Hauer & Stanford 1982). For example, the middle Green River, formerly a warm, turbid stream with endemic cyprinids, has changed

Table 1. Major ion concentrations (mg l^{-1}) at Lee Ferry before impoundment of Lake Powell and in water discharged from the hypolimnion (after Gloss *et al.* 1981)

	Colorado River at Lee Ferry 1948–62	Lake Powell discharge 1972–75
Ca^{2+}	81.8	73.6
Mg^{2+}	24.2	24.9
Na^{+}	68.4	75.7
K^{+}	4.2	4.1
HCO_3^-	189.0	159.0
$SO_4^=$	218.0	241.0
Cl^-	46.9	51.1
Total	633.0	629.0

with regulation by Flaming Gorge Dam to a cold, clear trout stream. However, side-flows from the Yampa and White rivers (Fig. 1) re-establish conditions favourable to the native fish (Vanicek *et al.* 1970). In fact, the Green River below the Yampa River, and the Colorado River from Lake Powell upstream to Glenwood Springs, Colorado, are the only reaches of the system where the lotic environment resembles historical conditions. In much of the Colorado drainage, reservoirs are so closely spaced that the nature of upstream impoundments determines that of downstream reservoirs, as well as the intervening rivers (Stanford & Ward 1986b).

The ecology of the virgin Colorado is largely a matter of speculation. The headwaters in many places remain as pristine rhithron streams with diverse zoobenthic communities and trout. The environment became increasingly hostile downstream, due to aridity and erosion. The riverine algae probably were diverse (cf. Czarnecki & Blinn 1978; Carothers & Minckley 1981), but scarce due to scouring by turbid flood-waters (Woodbury *et al.* 1959). Nutrient concentrations were sufficient for considerable plant growth during clearwater flows (cf. Fisher *et al.* 1982). The zoobenthos, adapted to shifting, sandy bottoms (Ward *et al.* 1986), with autochthonous and allochthonous detritus, supported a unique fishery (Stanford & Ward 1986a).

The post-regulation Colorado River is characterised by increased salinities, reduced temperature fluctuations, armoured substrata with profuse algal growths (mainly *Cladophora glomerata*), zoobenthos of low diversity and varying productivity, and a diverse fish fauna. The different river segments are influenced by upstream reservoirs, the length of river between reservoirs, and side-flow influences. Regulation and competition with introduced species has reduced native fish populations such that some of the unique, endemic species face extinction (Stanford & Ward 1986a).

Ecology of riparian systems

Riparian communities

Streams often are heterotrophic communities, dependent on allochthonous leaves and woody debris (Hynes 1975; Meehan *et al.* 1977). However, in the xeric environments of the American Southwest the streamside canopy is limited. Allochthonous material from deciduous broadleaf trees and shrubs may be an important energy source in some headwater streams (cf. Stanford & Ward 1984), but lotic environments in the Colorado Basin tend to be autotrophic (cf. Minshall 1978). Primary productivity is largely controlled by nutrient renewal from seasonal spates, especially in the desert streams of the Lower Basin (Busch & Fisher 1981; Fisher *et al.* 1982). Nonetheless, the riparian habitats of the Colorado River are strongly associated with fluvial processes, and are principal components of the ecosystem.

As most of the Colorado flows through semi-arid and desert lands, the riparian community may be the only significant vegetation in some areas. The riparian zone varies from a few metres in dry canyons to a kilometre or more on the floodplain of the lower mainstem, where extensive marshes occur (cf. Brown *et al.* 1977; Minckley 1973). The zone is vital as a source of particulate organic matter for the river community, and as cover and a forage area for many birds (Carothers *et al.* 1974; Anderson & Ohmart 1977; Stevens *et al.* 1977), herpetofauna (Carothers & Johnson 1983), rodents (Anderson *et al.* 1977) and other wildlife (Brinson *et al.* 1981). At higher elevations these habitats are a wintering area for mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*). Thus, although limited in total area, the longitudinally and locally variable stream bank vegetation (with zones around parts of the reservoirs) is an important part of the biophysiography of the American Southwest.

Riparian communities along the smaller streams are difficult to classify, because higher elevation climax associations may intergrade with streamside vegetation on broad floodplains, or riparian species may merge with woodlands on the sides of steep canyons. However, there are several generalised classes of plant communities (Stanford & Ward, pers. obs.; Lowe 1964; Brown *et al.* 1977):

Montane deciduous scrub
Above 2000 m, riparian communities in the Upper Basin and upper Gila River are dominated by broadleaf species usually near or overhanging the channel. These include willows (*Salix* spp.), alder (*Alnus tenuifolia*), dogwood (*Cornus stolonifera*), birch (*Betula occidentalis*), elder berry (*Sambucus glauca*), Rocky Mountain maple (*Acer glabrum*) and, in local areas, hawthorn (*Crataegus erythropoda*). In autumn, leaves from these plants are a major energy source for the stream communities. The association intergrades with pinyon (*Pinus edulis*), juniper (*Juniperus* spp.), sagebrush (*Artemisia tridentata*), scrub oak (*Quercus*

gambelli) and ponderosa pine (*Pinus ponderosa*) at lower, drier elevations, or with aspen (*Populus tremuloides*), spruce (*Picea engelmannii*, *P. pungens*) and fir (*Abies lasiocarpa*) in the more mesic areas (2700 m to the timberline at 3700 m). Strictly alpine willow species (e.g. *Salix antiplasta*) and small annual forbs (e.g. *Ranunculus* spp.) and sedges (*Carex* spp.) grow along the alpine streams.

Temperate deciduous forest

At about 2000 m a climax community of cottonwood (*Populus* spp.) and willows intergrades with the montane scrub. Cottonwood–willow associations dominate along the large tributaries and the Colorado mainstem from foothills to delta. In the Upper Basin, willows (*Salix caudata*, *S. amygdaloides* and others) form hedgerows along the channels, and galleries of cottonwoods (*P. wislizeni*, *P. augustifolia*) occur on more stable areas. The cottonwoods often are dense stands of trees more than 200 years old, and contribute a large leaf fall to the rivers. In drier reaches of the Upper Basin the cottonwood–willow fringe may be sparse and interspersed with grease wood (*Sarcobatus vermiculatus*) and salt bush (*Atriplex nutallii*), typical of lower elevations on the Colorado Plateau. In the Lower Basin similar dominants occur, but with *Salix gooddingii*, *S. bonplandiana* and other willows in association with the cottonwoods *Populus fremontii* and *P. augustifolia*. Some temperate deciduous communities in the interior of Arizona (Gila drainage) are mixed stands of sycamore (*Platanus wrighti*), ash (*Fraxinus pennsylvanica velutina*), boxelder (*Acer negundo*) and walnut (*Juglans major*), with the cottonwood–willow complexes. These are generally at middle altitudes (1000–2000 m), and intergrade with montane scrub. Stands exist also as hanging gardens along springbrooks which cascade over incisions in the walls of the Lower Basin canyons. Of course, this community is distinct from the similarly-named association in the New England area.

Subtropical deciduous woodland

This association is in the lower Gila drainage, where floodplain groundwaters at tributary confluences support mesquite (*Prosopis juliflora velutina*) bosques. These intergrade with Sonoran Desert plants along the San Pedro, Santa Maria, Verde and middle Gila rivers.

Subtropical evergreen forest

Relictual stands of California fan palm (*Washingtonia filifera*), of Miocene or Pliocene origin, occur at salt springs along ephemeral streams in the Sonoran Desert.

Colorado River marshes

Various wetlands occur, with plant associations reflecting the alkalinity and availability of water. In more xeric, saline systems saltgrass (*Distichilis stricta*) and alkali bulrush (*Scirpus paludosus*) are prevalent. On the lower Colorado River, reeds (*Phragmites communis*) are well developed. In more mesic systems, rushes (*Juncus* spp.), sedges (*Carex* spp.), bulrushes (*Scirpus* spp.) and cattails (*Typha* spp.) occur around open waters containing hydrophytes (e.g. *Potamogeton* spp., *Zannichellia palustris*, *Elodea canadensis*; cf. Minckley 1973; Carothers & Minckley 1981).

Desert canyon scrub

Riparian plants occur in the desert canyons above and below Lake Powell, a habitat that historically was reliant on seasonal flooding. Fast-growing species like arrow-weed (*Pluchea sericca*), groundsel (*Baccharis* spp.) and willows occupy the flood zone. Beyond is a terrace created by extreme floods (Fig. 7), populated by Apache plume (*Fallugia paradoza*), redbud (*Cercis occidentalis*), hackberry (*Celtis reticulata*), mesquite (*Prosopis juliflora*) and acacia (*Acacia greggi*). Typical desert plants (e.g. brittlebrush, *Encelia forinosh*; cacti, *Opuntia* spp.; creosote bush, *Larrea tridentala*) intergrade with riparian plants on the canyon walls (Carothers *et al.* 1979).

Impacts of stream regulation and salt cedar invasion

The pristine associations have been affected by over-grazing (cf. Dobyns 1978), logging of cottonwoods to fuel river steamers (Ohmart *et al.* 1977) and stream regulation. Now there are merely over-mature remnants of the great cottonwood galleries (particularly *Populus fremontii*), once more than a kilometre wide on either side of the lower Colorado and on islands in the delta (Ohmart *et al.* 1977; Stanford & Ward 1984). Most mesquite bosques have disappeared as water tables recede along the lower Gila River (Brown *et al.* 1977). By far the greatest change has been the invasion of a deciduous Eurasian tree, the salt cedar (*Tamarix chinensis*). This species is adapted to saline soils, and in 50 years has invaded all but montane riparian habitats. The trees grow to 10–12 m, often as dense stands, and the seedlings are hardy and readily displace native plants on scoured floodplains. The interactions with native species are not well understood (Everitt 1980), and are complicated by flow regulation.

Photographs of riparian sites in the Grand Canyon between 1870–1930 show that salt cedar invaded the canyon before construction of Lake Powell. However, post-regulation discharges have greatly encouraged its proliferation (Turner & Karpiscak 1980). Prior to regulation, seasonal flooding scoured the riparian land and, although many species could colonise the land between floods, none assumed dominance. Since regulation, flows have allowed salt cedar to assume dominance or subdominance (Fig. 7a). This is seen also in the Upper Basin, where tangles of salt cedar and willow predominate. Old

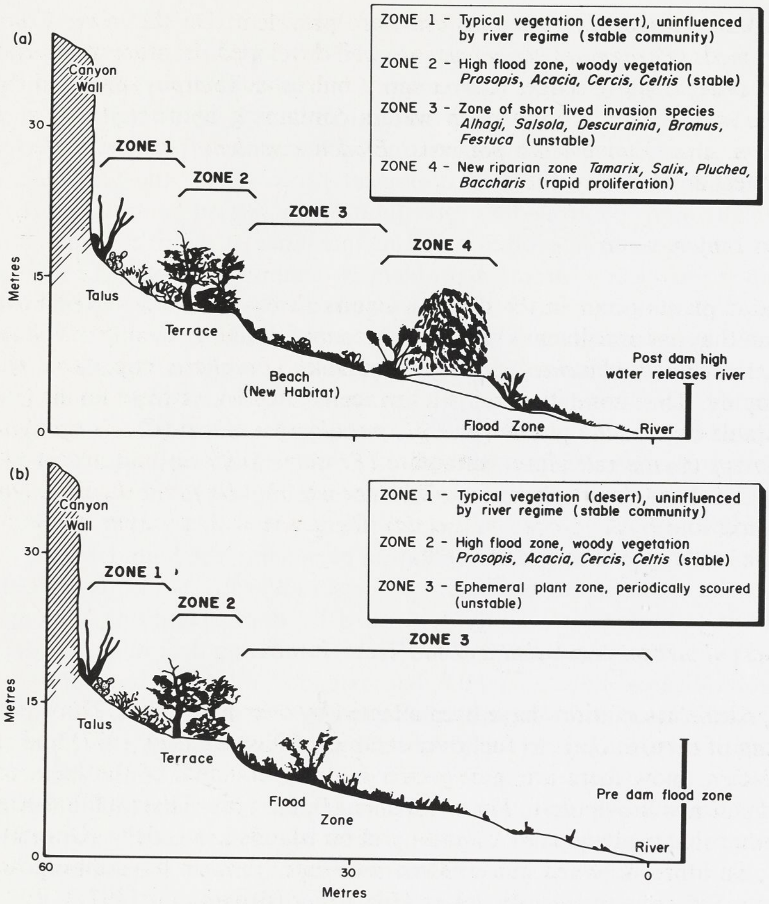


Figure 7. Impact of stream regulation on the riparian ecosystem in the Grand Canyon of the Colorado River: (a) after regulation by Lake Powell, (b) pristine conditions (after Carothers *et al.* 1979).

cottonwoods remain but are over-mature, with seedlings unable to mature in the salt cedar-willow understory (cf. Stanford & Ward 1984).

These changes also impact the riparian fauna: some species are extirpated or reduced in numbers, while others gain advantages from the dense vegetation of stabilised streambanks (thus beavers, *Castor canadensis*, now are abundant in the Grand Canyon: Carothers & Johnson 1983). Increased aquatic productivity imposed by regulation also may provide supplementary food for terrestrial animals. In the Grand Canyon, algae and amphipods (*Gammarus*) are entrained as discharges change with power operations. The amphipods are caught in pools and backwaters, providing food for birds and, surprisingly, a desert lizard (*Cnemidophorus* spp.; Carothers & Johnson 1983).

Ecosystem perspective

The management of river ecosystems is made difficult by a lack of basic knowledge. Our understanding of natural streams is confounded by the fact that few, if any, rivers remain pristine in the sense of being unaffected by man. Although it is clear that ecological processes on the Colorado delta historically were controlled by precipitation in distant mountains, the biophysical interactions in evolution and maintenance of the river's unique fauna are much less clear. The main problem is defining an ecological time scale. Twenty-five thousand years ago the Colorado River was a system of lakes regulated by river segments in which the native fauna diversified. Today, the river exists as segments regulated by reservoirs in which an exotic fauna predominates. This has happened in less than 100 years. Modern man is an inexorable element in the Colorado River ecosystem, but recall that his first view of the system revealed the vestiges of a still earlier community of stream regulators. Lessons in all manner of science are implicit in the regulation of the Colorado River.

We have argued that stream regulation by some of the high dams may serve to test hypotheses about ecosystem processes (Ward & Stanford 1983, 1984). Reservoir tailwaters are tightly controlled by dam operations, and may be treated as an experimental microcosm by manipulating the timing and depth of reservoir releases. Paulson (1983) has extended this idea to control of the biophysical processes in downstream reservoirs by manipulation of upstream impoundments. Such approaches should permit significant contributions to limnology, and clarify the site-specific impacts of regulation. Whether such information will help maintain endangered fauna is unclear (many fish populations probably are beyond salvation), but it may test the ecological validity of manipulations under the guise of resource management (e.g. salinity control projects and the enhancement of reservoir productivity).

Rhetoric about the consequences of regulation in the Colorado River involves two major issues: (a) whether there is enough water to maintain desirable ecosystem attributes and (b) whether native and exotic fish can coexist. It appears that the answer on both counts is no. Consumptive use presently is allocated more water than the basin produces, compared to the estimated virgin flow. By the year 2000, deficits will occur whether or not additional developments occur (Spofford 1980). Severe water shortages, as always in the history of man, will preclude allocation of stream flows for fish or other ecological concerns. Some endemic fish may be cultured in hatcheries (e.g. squawfish: Hammon & Inslee 1982), but attempts to re-introduce native species to their former ranges (Miller *et al.* 1982) probably will fail. That some species (man included) fail while others proliferate in ecosystems undergoing change is tempered only by the time-frame within which one chooses to pose the problem.

Acknowledgements

We thank Drs L. Paulson and R. Behnke for reviewing the manuscript.

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9A. Reservoirs of the Colorado system

J. A. Stanford & J. V. Ward

Introduction

The insatiable demand for irrigation and potable water in the arid American Southwest has spawned hundreds of reservoirs to regulate virtually the entire Colorado River. These vary in area from less than one hectare in high altitude, headwater segments to more than 650 km^2 in lowland, mainstem segments (e.g. Lakes Powell and Mead; Stanford & Ward 1986a: Fig. 1). The limnology of these reservoirs is complex because the sub-basins encompass myriad geomorphic and hence physico-chemical characteristics. For example, many headwater reservoirs are in predominantly granitic or volcanic (basaltic) formations and are ion-deficient, producing substantially less biota than those in the nutrient-rich sedimentary formations downstream. The limnology of individual reservoirs is poorly known, although government agencies have open-file reports of water storage and fisheries data for most large impoundments. Detailed studies of the four largest mainstem reservoirs have produced important insights into the trophic status and dynamics of dissolved solids in deep storage reservoirs. Here we attempt to summarise the major findings of these studies, and demonstrate the complexity and upstream–downstream linkage of limnological processes.

Influence of Lake Powell on Lake Mead

The impact of regulation is most profound in the large, desert reservoirs of the Lower Basin. The hydrology and ecology of these environments are determined by the timing, volume and quality of waters delivered from distant mountain areas, from upstream reservoirs and infrequent, intense local storms (Rinne 1975). By the time water reaches the Lower Basin, salt levels have increased by two orders of magnitude, and evaporation further compounds this problem (Pillsbury 1981). Except on the lower Green River and the Colorado from the

The Ecology of River Systems, edited by B. R. Davies & K. F. Walker

Table 1. Morphometry of reservoirs in the Colorado River Basin

	Mead	Powell	Flaming Gorge	Mohave
Surface area (km^2)	660	653	170	115
Volume (km^3)	36.0	33.3	4.7	2.3
Maximum depth (m)	180	171	133	42
Mean depth (m)	55	51	27	20
Shoreline development	10	26	19	3

Gunnison River to Lake Powell, reservoirs are so closely spaced that those upstream profoundly affect the limnological nature of those downstream. This occurred when Lake Powell was formed 450 km upstream from Lake Mead, providing a classic lesson in reservoir limnology.

Lake Mead, impounded in 1935, was the first deep reservoir in the Colorado drainage, and remains the largest (Table 1). Until construction of Lake Powell in 1963, the inflowing Colorado River exercised advective control over development of the thermocline and nutrient dynamics (Anderson & Pritchard 1951; Saur & Anderson 1956). In winter the river, being relatively cold and dense, entered as an underflow, and in autumn and spring the density plume tended to interflow. In spring, sediment loads associated with floods created intense overflow plumes (Anderson & Pritchard 1951). In most years spring overflow currents from the river carried suspended clays as far as Boulder Canyon, a narrow point in Lake Mead that defines upper (Virgin) and lower (Boulder) basins. Mayer & Gloss (1980) showed that the clays buffer dissolved phosphate in the reservoir water: as dissolved phosphate is utilised by micro-organisms, additional phosphate is desorbed from the clays. The river inflow also fertilised Lake Mead with nitrate and, as a consequence, production was much higher in the Virgin Basin than the Boulder Basin (Table 2). Enrichment increased in 1955–62 due to intense flooding, which redistributed the reservoir sediments (Prentki & Paulson 1983) and promoted rapid growth of the introduced threadfin shad (*Dorosoma petenense*), supporting a productive fishery for another introduced fish, the largemouth bass (*Micropterus salmoides*; Paulson *et al.* 1979).

In 1963 the impoundment of Lake Powell created a dendritic reservoir deeper than Lake Mead (Table 1). Primary productivity in Lake Powell is phosphorus-limited and dependent on the intrusion of river waters and advective circulation of suspended sediments. The San Juan Arm is more productive than the Colorado Arm because the San Juan River carries higher phosphorus- and nitrogen-enriched sediment loads. Gloss *et al.* (1981) estimated that 6260 t of total phosphorus annually enter Lake Powell, but only 229 t exit through Glen Canyon Dam. Therefore, only 198 t P a^{-1} now reach Lake Mead (Prentki & Paulson 1983), indicating a 98% decrease in loading. Phosphorus sedimentation

Table 2. Phytoplankton production ($kt\,a^{-1}$) in Lake Mead before (1936–54, 1955–62) and after (1963–81) construction of Lake Powell. Data from rates of organic carbon deposition regressed on productivity (after Prentki & Paulson 1983)

Years inclusive	Whole reservoir	Boulder Basin	Virgin Basin
1936–54	146	0.6	117
1955–62	651	43	395
1963–81	144	73	44

in Lake Mead decreased 93.5% after construction of Lake Powell (Prentki *et al.* 1981), compared with an estimated retention of 96.3% in Lake Powell (Gloss *et al.* 1981).

With reduced nutrient loading *via* the Colorado, lake-wide primary production in Lake Mead now is 4.5 times lower than in 1955–63, before regulation by Lake Powell (Table 2). The loss of productivity would be more dramatic except that nutrient loading occurs *via* sewage discharged to Las Vegas Wash in the Boulder Basin (Baker & Paulson 1981; Paulson & Baker 1981). The Boulder Basin now yields 51% of the reservoir's annual production (Table 2), whereas it produced seven percent prior to Lake Powell (Prentki & Paulson 1983).

Threadfin shad populations in Lake Mead have declined dramatically in recent years (Baker & Paulson 1983), and predatory game fish also have suffered. Rinne *et al.* (1981) demonstrated a correlation between shad production and chlorophyll levels in the Salt River reservoirs of the Gila drainage (see also Johnson 1970, 1971). The declining fertility of Lake Mead, due to Lake Powell, appears responsible for the poor condition of the fishery. However, striped bass (*Morone saxatilis*), a piscivore, was introduced into Lake Mead in 1969 and reproduced naturally until recently; Baker & Paulson (1983) reported that large specimens were rare and most fish were in poor condition, apparently for lack of food. Over-exploitation of the shad food base may have compounded the problem of decreasing productivity.

Salinity and nutrient dynamics

Circulation patterns and nutrient dynamics in the larger impoundments are influenced by salinity. Haloclines occur at least seasonally in the 12 largest reservoirs, because they impound saline flows or overlie saline formations, or both. Their complex morphometry (Table 1), particularly the precipitous shorelines in canyons near the dams, limits wind-induced circulation. Lakes Mead and Powell and other reservoirs in the Lower Basin have been referred to as warm-monomictic (Stewart & Blinn 1976), whereas those of the Upper Basin are dimictic. However, Bolke (1979) reported a persistent halocline near the dam at Flaming Gorge Reservoir, indicating meromixis.

A similar but more widespread halocline occurs in Lake Powell. Fifty-three percent of the shoreline is near-vertical cliffs and, due to lack of wind circulation, there is a monimolimnion from the dam to the upper reaches of the reservoir. Convective circulation penetrates only to about 60 m (Johnson & Merritt 1979), and oxygenation of the bottom water depends entirely on advective circulation generated by saline underflows from the Colorado and San Juan rivers during low winter discharge (Johnson & Page 1981). Metalimnetic oxygen depletion (negative heterograde profile) occurs virtually lake-wide in late summer (Stewart & Blinn 1976; Johnson & Page 1981); anoxia presumably is caused by decomposition of senescent phytoplankters which accumulate on the chemocline after settling from the mixolimnion (Hansmann *et al.* 1974; Johnson & Page 1981). Metalimnetic oxygen stagnation begins in the bay mouths and temporally develops towards the dam. Convective circulation becomes general in early winter (Johnson & Page 1981).

The depth of convective circulation and halocline formation in Lake Powell is marked by a strong withdrawal current at *c.* 50–60 m (Johnson & Merritt 1979). Because of re-oxygenation by winter river underflows and trapping of organic matter in the metalimnion, the monimolimnion remains aerobic. This limits nutrient mobilisation from the sediments, and nutrients released by mineralisation are not returned to the epilimnion for the lack of convective circulation (Gloss *et al.* 1980, 1981). Calcite precipitation also may scavenge dissolved substances, particularly phosphate, *via* adsorption (Reynolds 1978). Thus, there is a persistent nutrient-deficiency in the euphotic zone. Production in Lake Powell is phosphorus-limited and dependent on seasonal advective nutrient renewal *via* the spring overflow of the river turbidity plume (Gloss *et al.* 1980).

Production in most, if not all, Colorado River reservoirs is controlled primarily by the physico-chemical properties of river inflows. Except in the headwaters region, the inflows are laden with nutrient-rich sediments. However, most of the nutrients are not mobilised by microbial metabolism due to strong absorption gradients (e.g. phosphorus sorption on sediment or calcite particles), or are not recycled from the tropholytic zone, as described above. Steady-state retention coefficients for total nitrogen and phosphorus in Lake Powell are estimated as 0.086 and 0.963 respectively (Gloss *et al.* 1981), indicating great differences in the conservation of these elements by processes in the reservoir. It is not surprising that these systems do not fit the empirical models used to predict eutrophication from nutrient loading (LaBough & Winter 1981; Mueller 1982).

Eutrophication is a lesser problem than increasing salinity (Bishop & Porcella 1980). Most of the reservoirs are located far from agricultural areas or urban centres, although some bays in Lake Powell are affected by human activities

(Hansmann *et al.* 1974), and eutrophication of Las Vegas Bay in Lake Mead is documented (Paulson & Baker 1981). Seasonal phytoplankton succession in Lake Powell involves a spring diatom pulse (*Fragillaria crotonensis* and *Asterionella formosa*), a diverse summer community (*Dinobryon sertularia* and Chloroccocales), a late autumn diatom pulse (*Synedra delicatessima* var. *augustissima*) and no abundant winter forms (Stewart & Blinn 1976). This sequence does not indicate general nutrient enrichment.

Bolke (1979) reported blooms of blue–green algae (*Anabaena, Oscillatoria* and *Anacystis*) associated with oxygen depletion in Flaming Gorge Reservoir. This appears to be the most eutrophic of the large reservoirs in the system, and a recent refit to permit epilimnial releases for downstream temperature control (Stanford & Ward 1986b) may exacerbate problems by retaining nutrients previously lost in outflow from the hypolimnion.

The contribution of the reservoirs to salinity problems in the Colorado Basin usually is blamed on evaporation and dissolution of salts (cf. Pillsbury 1981). While evaporation rates are high (*c.* $987\,000\,m^3\,a^{-1}$ in Lake Mead: Paulson 1983), salt losses also occur *via* calcite precipitation (Reynolds 1978). Gypsum dissolution is high after initial flooding (Table 2), but weakens as deposits are buried by sediment (Bolke 1979; Gloss *et al.* 1981; Paulson & Baker 1983). Stanford & Ward (1983) showed that reservoirs on the Gunnison River effect a net reduction of major ion concentrations, and Paulson & Baker (1983) drew similar conclusions for Lakes Mead and Powell. Paulson (1983) showed that cold water from Lake Powell has reduced the net heat budget of Lake Mead, causing less evaporation and an average salinity decrease of at least $9\,mg\,l^{-1}$, and suggested that control would be enhanced if water were discharged from the surface rather than the hypolimnion. This would also retain nutrients and perhaps stimulate productivity; in turn, this would encourage calcite precipitation, providing a secondary control mechanism.

Reservoir fisheries

Reservoirs have favoured exotic fish at the expense of populations of native species honed for survival in the uncompromising environment of the virgin Colorado River (Stanford & Ward 1986b). In many of the reservoirs highly touted sport fisheries have been created (cf. Hoffman & Jones 1973), although these have waxed and waned with changes in reservoir trophic status caused, for example, by reductions in nutrient dissolution in the basin with age, and loss of nutrients to new reservoirs upstream. Operational changes (Hoffman & Jones 1973; Morgensen 1983) and competitive interactions due to introductions (stocking) or invasions (immigration) of new species also have negatively impacted the sport fisheries.

In addition to the case of striped bass in Lake Mead (see above), an example of the "boom and bust" nature of Colorado River fisheries occurred in Flaming Gorge Reservoir. Rainbow and brown trout were introduced in 1962, immediately after the reservoir was filled. The annual harvest exceeded 800 t by 1965, and there were abundant specimens exceeding 10 kg. Natural reproduction was limited for lack of suitable spawning areas, but despite intensified stocking and gradually declining fishing pressure, the annual harvest steadily declined to less than 74 t in 1979 (Varley *et al.* 1971; Schmidt *et al.* 1980). The reasons for senescence of the fishery are unclear but undoubtly involved the changing trophic status of the reservoir, habitat limitations imposed by anoxic waters below the halocline, and over-exploitation of forage fish by the salmonids. The situation might be improved by introduction of a forage fish able to utilise the pelagic areas of the reservoir, although trial introductions of threadfin shad, so successful as forage for striped bass in the Lower Basin reservoirs, have failed in the cold waters of Flaming Gorge (Schmidt *et al.* 1980).

In many of the Colorado's reservoirs density and withdrawal currents interact with other limnological phenomena (e.g. metalimnetic oxygen stagnation in Lake Powell) to restrict fish migrations. In Lake Mohave a "two-story" fishery exists: continual underflow of well-oxygenated, cold waters from the hypolimnion of Lake Mead entrains seston and provides a refugium for salmonids, while bass, shad and other warm-water fish reside above the density current (Priscu *et al.* 1981; Dr L. Paulson, Univ. Nevada at Las Vegas, pers. commun.).

Conclusion

The reservoirs of the Colorado system have complex morphologies, are greatly influenced by their inflows, and exist in arid environments that, under natural conditions, would not sustain lentic waters of such size. They are serial retention basins, trapping sediments and dissolved solids that prior to regulation must have fertilised the backwaters along the mainstem river and the delta estuary. Reservoir productivity at all trophic levels may be related to processing of the nutrients imported by river inflows.

Most of the reservoirs are rapidly filling with saline sediments. Gould (1954) showed that about 30% of the volume of Lake Mead was lost to sediment within 13 years of impoundment, but this load is now being contained primarily in Lake Powell. Under these circumstances, total phosphorus retention coefficients are unusually high. In the deep reservoirs haloclines are common and limit the circulation of solutes and gases. These processes in general lead to phosphorus limitation of primary production. Advective, rather than convective circulation may be most important in regenerating phosphorus in the euphotic zone.

The reservoirs are so closely spaced that processes in downstream impoundments may be primarily controlled by the depth, pattern of discharge and physico-chemical attributes of upstream reservoirs. Perhaps, as the reaches between successive reservoirs shorten with new constructions, the Serial Discontinuity Concept, devised by Ward & Stanford (1983) to predict the recovery of lotic systems below dams, might be modified to encompass a serial response in lentic trophic status imposed by linkage of reservoir systems.

The Colorado is a desert system showing pronounced annual variations in water yield, undermining the predictability of limnological phenomena in its reservoirs. This, with the unpredictable consequences of competition among native and introduced fish and other biota, should lead investigators to expect the unexpected. Witness, for example, the sudden bloom of jellyfish (*Craspedacusta sowerbyi*) that occurred in Lake Mead when a long period of stable levels was interrupted by record levels (Deacon & Haskell 1967).

Acknowledgement

We are grateful to Dr Larry Paulson for help in preparing this manuscript.

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9B. Fish of the Colorado system

J. A. Stanford & J. V. Ward

Introduction

The abundant remains of large minnows (Cyprinidae) in caves near desert segments of the Colorado system (Plate 1c, e; cf. Minckley 1973), suggest that the riverine fish were important sustenance for prehistoric man. The river continues to supply sustenance, but the modes of transfer have changed dramatically. The vicarious regulation of the Colorado River, coupled with many introductions of non-native species, has caused precipitous declines among the indigenous fish.

This chapter describes the indigenous fish fauna and its relation to the physiographic and hydrographic history of the basin (Stanford & Ward 1986a: Fig. 1), and includes consideration of species in parts of the Colorado system affected by desertification (e.g. Pluvial White River, Railroad Valley: Hubbs & Miller 1948). We also indicate the status of the native fish in the regulated river, and discuss the impacts of exotic species.

The native fish fauna

Thirty-two species of fish in seven families are indigenous to the Colorado system (Table 1). Several have diversified in isolated local or sub-basin populations. Thus, four forms of the Colorado River chub (*Gila robusta*) are recognised in the Gila, Virgin and Pluvial White rivers (Rinne 1976; Smith *et al.* 1979). Two subspecies of the spinedace (*Lepidomeda mollispinis*) are isolated in the Virgin River and Meadow Valley Wash (Lee *et al.* 1980). Minckley (1973) listed four subspecies of the desert sucker (*Catostomus clarki*) in Lower Basin tributaries. Five subspecies of White River springfish (*Crenichthys baileyi*) are isolated in desert springs in the Pluvial White and Moapa drainages (Deacon & Bradley 1976; Williams & Wilde 1981). The speckled dace (*Rhinichthys osculus*) is the most widespread native species, but populations in different sub-basins

The Ecology of River Systems, edited by B. R. Davies & K. F. Walker

Table 1. Indigenous fish of the Colorado system, showing preferred habitats and historical distributions (after Miller 1958; Smith 1978; Minckley 1973, 1979; Rinne 1976; Deacon 1979; Behnke & Benson 1980; Tyus *et al.* 1982). The status of species is extinct (EX), in danger of extinction (ED), threatened (TH), restricted (R) or widespread (WS) (after Deacon *et al.* 1979; Bishop & Porcella 1980; Williams 1978; Tyus *et al.* 1982). Endemic species are designated EN. Taxonomy and common names are according to Lee *et al.* 1980; species indicated by an asterisk (*) include two or more subspecies.

FAMILY genus	Common name	Status	Preferred habitat	Historical distribution
SALMONIDAE				
*Salmo clarki** Richardson	Colorado R cut-throat trout	TH	Rhithron streams	Upper Basin
S. apache Miller	Arizona trout	TH, EN	Rhithron streams & beaver ponds	Gila (Salt) & Little Colorado R headwaters
S. gilae Miller	Gila trout	ED, EN	Rhithron streams & beaver ponds	Gila (Verde & Gila) R headwaters
Prosopium williamsoni (Girard)	Mountain whitefish	R	Rhithron streams	Green R headwaters
CYPRINIDAE				
Gila elegans Baird & Girard	Bonytail chub	ED, EN	Pool-run areas in swift canyon segments	Mainstream & big river tributaries
G. cypha Miller	Humpback chub	ED, EN	Eddy/run interfaces in deep swift canyons	Mainstream & big river tributaries
G. intermedia (Girard)	Gila chub	R, EN	Small streams and ciengas	Gila R
*G. robusta** Baird & Girard	Roundtail chub	WS, EN	Deep runs & backwaters	Mainstream & big river tributaries
Lepidomeda vittata Cope	Little Colorado R spinedace	R, EN	Pools below gravel riffles	Little Colorado R
L. albivallis Miller & Hubbs	White R spinedace	ED, EN	Cool (18–22°C) desert springs	Pluvial White R

Table 1. Continued.

FAMILY genus	Common name	Status	Preferred habitat	Historical distribution
L. altivelis Miller & Hubbs	Pahranagat spinedace	EX, EN	Clear, moderately swift outflows of springs	Pluvial White R
*L. mollispinis** Miller & Hubbs	Virgin R spinedace	ED, EN	Pool/run areas in moderately swift channels	Pluvial White R
Meda fulgida Girard	Spikedace	TH, EN	Shallow riffles & eddies	Gila R
Moapa coriacea Hubbs & Miller	Moapa dace	ED, EN	Shallow riffles & pools	Moapa R
Agosia chrysogaster Girard	Longfin dace	WS	Sandy bottoms in smaller, hot desert streams	Gila & Bill Williams R
Plagopterus argentissimus Cope	Woundfin	ED, EN	Swift riffles of turbid, big river segments	Lower mainstem, Virgin & Gila R
Ptychocheilus lucius Girard	Colorado R squawfish	ED, EN	Deep runs & backwaters	Mainstem & big river tributaries
*Rhinichthys osculus** (Girard)	Speckled dace	WS	Shallow, swift riffles with gravel or rubble substrata	Mainstem & all tributaries
Tiaroga cobitis Girard	Loach minnow	R, EN	Gravel riffles in smaller rivers & streams	Gila R
CATOSTOMIDAE				
Xyrauchen texanus (Abbott)	Razorback sucker	ED, EN	Backwaters, quiet eddies and deep runs	Mainstem & big river tributaries
Catostomus latipinnis Baird & Girard	Flannelmouth sucker	WS, EN	Runs, shorelines & eddies	Mainstem & big river tributaries
C. discobolus (Cope)	Bluehead sucker	WS	Deep riffles & runs over gravel/cobble substrata	Upper Basin tributaries & Grand Canyon

Table 1. Continued.

FAMILY genus	Common name	Status	Preferred habitat	Historical distribution
*C. clarki** Baird & Girard	Desert sucker	WS, EN	Pool/riffle areas in warm streams	Lower Basin tributaries
C. insignis Baird & Girard	Gila sucker	R, EN	Quiet, deep pools with rocky substrata	Gila & Bill Williams R
C. platyrhynchus (Cope)	Mountain sucker	R	Rocky pools & riffles in rhithron streams	Green R
COTTIDAE				
Cottus bairdi Girard	Mottled sculpin	WS	Riffles & deep runs in rhithron streams	Upper Basin tributaries
C. beldingi Eigenmann & Eigenmann	Piute sculpin	R	Swift riffles in rhithron streams	Headwater tributaries to upper mainstem
CYPRINODONTIDAE				
Cyprinodon macularis Baird & Girard	Desert pupfish	ED	Springs, pools & marshes of desert streams & backwaters of big river channels	Lower Basin mainstem, Gila R & Salton Sea
*Crenichthys baileyi** (Gilbert)	White R springfish	ED, EN	Desert springs	Moapa & Pluvial White R
C. nevadae Hubbs	Railroad Valley springfish	R, EN	Desert springs	Pluvial White R
POECILIDAE				
*Poeciliopsis occidentalis** (Baird & Girard)	Gila top minnow	ED	Shallow areas of virtually all desert aquatic habitats	Lower Basin mainstem, Gila R, Salton Sea
MUGILIDAE				
Mugil cephalus Linnaeus	Striped mullet	R	Marine migrants into deep runs & backwaters	Lower mainstem & Salton Sea

vary in morphometry, meristic characters and ecology (Hubbs *et al.*, 1974); four subspecies are present in the Lower Basin and two in the Upper Basin (Deacon *et al.* 1979; Williams 1978; Behnke & Benson 1980). The Colorado River cut-throat trout (*Salmo clarki pleuriticus*) is native to the headwaters of virtually all Upper Basin tributaries, and is one of 15 subspecies in the western United States tentatively recognised by Behnke (1981). An undescribed *Catostomus* related to *C. latipinnis* is isolated in the Little Colorado River (Minckley 1973). In all, 46 native fish (including subspecies) existed in the Colorado drainage prior to regulation; based on present taxonomy, thirty-eight (85%) are endemic.

High endemism is a salient biogeographic feature of Colorado River fish, reflecting diverse habitats from alpine streams to desert springbrooks (Miller 1958). The endemism is a result of the Quaternary history of fluctuating pluvial and interpluvial episodes in the intermountain area of western North America. Many genera and several extant species were present in Pliocene times, and radiated in Pleistocene drainages to the Colorado River (Smith 1978). Mainly subspecific differentiation occurred as populations were isolated by desertification in the Southwest (e.g. Pluvial White and Moapa rivers, Meadow Valley Wash, Las Vegas Wash and Little Colorado River). Smith (1978) evoked the concept of island biogeography (MacArthur & Wilson 1967) to illuminate the impact of isolation on pluvial fish in the intermountain area of western North America, including the Great Basin and the Colorado River. He noted that 51 of the 81 intermountain native fish occurred in only one sub-basin, and concluded that the present fauna is mainly a consequence of local extinctions within a Pleistocene fauna, rather than recent colonisation. Thirty-five percent of the Colorado River fauna is found only in the Virgin–Pluvial White system, and another 20% is endemic in the Gila drainage. However, only nine of 38 endemic Colorado River fish are found upstream of the Little Colorado River. Most of the Upper Basin fish (eight of 14 taxa) occur in adjacent drainages (e.g. Snake River), or were distributed into the Lower Basin at various times; one subspecies is endemic (*Rhinichthys osculus thermalis*: Behnke & Benson 1980). The dichotomy between the diverse Lower Basin fauna and a comparatively depauperate Upper Basin fauna (cf. Stanford & Ward 1986a: Fig. 1) reflects the influence of the Pleistocene Lake Haulapai, near the mouth of the Grand Canyon (Smith 1978). Isolating barriers were most prevalent in the xeric Lower Basin (Naiman 1981).

The fossil record also reflects a gradient (due to latitude and altitude) from the Upper to Lower basins (e.g. *Cottus* in the north, cyprinodontids in the south; Smith 1978). Clines in species distributions are evident in Upper (Lanigan & Berry 1981; Stanford & Ward 1984) and Lower Basin tributaries (LaBounty & Minckley 1972; Cross 1976). However, high-altitude headwater streams in the north (e.g. Gunnison River: Fig. 1a) contain a more stenothermic fauna than the south (cf. Gila River: Fig. 1b). For example, *Salmo gilae* survives late-summer temperatures up to 27°C in the Gila drainage (Lee & Rinne 1980), whereas *S. clarki pleuriticus* in the Upper Basin inhabits waters well below 20°C.

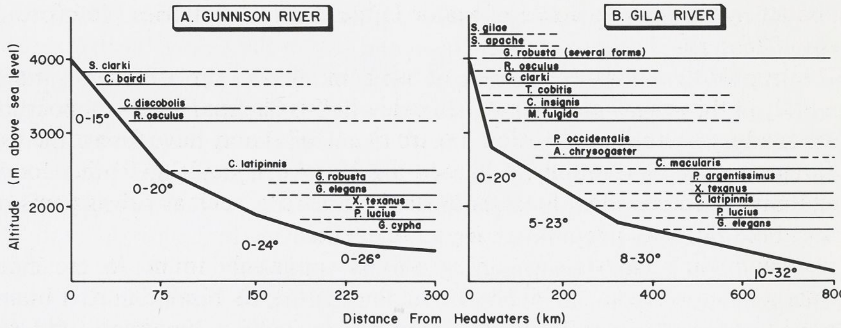

Figure 1. Altitudinal distribution of native fish in (A) the Gunnison River and (B) the Gila River before flow regulation. Approximate annual ranges in water temperatures also are shown (after Deacon & Minckley 1974; Dr R. Behnke, Colorado State Univ., pers. commun.; Stanford & Ward unpublished)

The distributions of *S. gilae* and *S. apache* in the Upper Gila River are like those of two morphologically distinct, more stenothermic forms of the minnow *Gila robusta*, perhaps indicating similar isolation mechanisms (Minckley 1973; Rinne 1976). Prior to regulation, the historical distribution of *Gila* in the Upper Basin barely overlapped the predominant range of *Salmo* (cf. Fig. 1a). Thus, the N–S latitudinal gradient interacts with altitudinal gradients in each sub-basin. In the south, desert conditions have advanced high into the tributaries, where isolated water bodies harbour a diverse endemic fauna adapted to a broad range of temperatures. In the north, wetter, less extreme environments favour species commonly found in adjacent drainages.

Prior to regulation, the native fauna of the mainstream river from the delta into Colorado and the Green River into its middle segment was limited primarily to six endemic minnows and suckers (Table 1, Plate 1): bonytail chub (*Gila elegans*), roundtail chub (*G. robusta*), humpback chub (*G. cypha*), squawfish (*Ptychocheilus lucius*), flannelmouth sucker (*Catostomus latipinnis*) and razorback sucker (*Xyrauchen texanus*). The non-endemic speckled dace (*Rhinichthys osculus*) also occurred throughout the mainstream. The woundfin (*Plagopterus argentissimus*) was limited to the Lower Gila and Virgin rivers. Desert pupfish (*Cyprinodon macularis*) were found primarily in backwaters and marshes. Roundtail chub and flannelmouth sucker were more common in areas above the confluence with the Virgin River. Several euryhaline marine species, including tenpounder (*Elops affinis*) and spotted sleeper (*Elotris picta*), apparently frequented the estuary and delta areas (Gilbert & Scofield 1898), but only striped mullet (*Mugil cephalus*) were abundant in the main channel (Minckley 1973, 1979). Thus, the predominant fauna of the lower main segment (Virgin River to below the Gila) was three species (squawfish, bonytail chub and razorback sucker; Minckley 1979). This reflects the severity of the environment prior to regulation. All big-river species except bonytail chub (Tyus *et al.* 1982) were abundant in the lower reaches of major Upper Basin tributaries (Stanford & Ward 1986a; Fig. 1).

The trophic structure of the big-river fish communities probably was simple, especially in the lower mainstream (Minckley 1979). The sparsity of zoobenthos in the sandy, unstable river bottom (Ward *et al.* 1986) may have forced the fish to forage in specific locations. Attached algae, insects, snails and other foods would have been prevalent in areas of stable substrata, such as debris dams or rock-rubble riffles and rapids in canyon segments.

The humpback chub (*Gila cypha*) now is commonly found in the most turbulent canyon streams (Valdez & Clemmer 1982); its bizarre nuchal hump (Plate 1a, c) may assist in swift waters by hydraulically maintaining the head near the substratum. Bonytail and humpback chub feed on zoobenthos and terrestrial insects, with algae and detritus (Vanicek & Kramer 1969), although bonytails are inclined to feed on drifting seston and may even subsist on plankton, as in Lake Mohave. Dense vegetation along the pristine river, with incessant desert winds, may have linked the ecology of bonytails with terrestrial production of insects, especially in the lower river where bonytails were once more common than humpbacks (Minckley 1979). Speckled dace, roundtail chub and flannelmouth suckers are omnivorous (Minckley 1973), but are more abundant in rubble areas harbouring algae and zoobenthos (Stanford unpublished). Razorback suckers (Plate 1d) have numerous gill rakers as a fine branchial sieve to trap seston and fine Aufwuchs. The keel-like antero-dorsal hump acts as a lateral stabiliser as the fish moves through the water with its mouth open, filtering fine detritus and plankton (Minckley 1973). Squawfish (*Ptychocheilus lucius*) were the top carnivores of this simple, uniquely specialised big-river fauna. Squawfish (Plate 1e) feed voraciously on other fish (Vanicek & Kramer 1969), and may attain 1.5–2.0 m and 35–45 kg (Miller 1961). Called "white salmon" in the Colorado Basin, the squawfish is one of the world's largest minnows (Minckley 1973).

Despite the simple food chain, the river alone could not provide a food base to support large populations of big fish such as squawfish and razorback suckers (Minckley 1979). Prior to regulation, numerous backwaters occurred throughout the range of the big-river fish. In aggraded segments of the Lower Basin extensive marshes were reworked and refilled during river spates (Sykes 1937; Dill 1944). These habitats probably subsidised the river trophic base by accumulating detritus and producing plankton and zoobenthos. All the big-river species use backwaters as refugia, nurseries and feeding areas (Minckley 1973; Valdez & Wick 1983). Valdez & Wick (1983) showed that radio-tagged squawfish and razorback suckers frequently move between mainstream and backwater, with a remarkable ability to sense the depth and location of the connecting channel (which often fills with sediment between floods, isolating the backwater). Backwaters and marshes in the Lower Basin also harboured large populations of the desert pupfish. Seasonal migrations of small mullet into the lower river probably provided additional prey for squawfish (Minckley 1979).

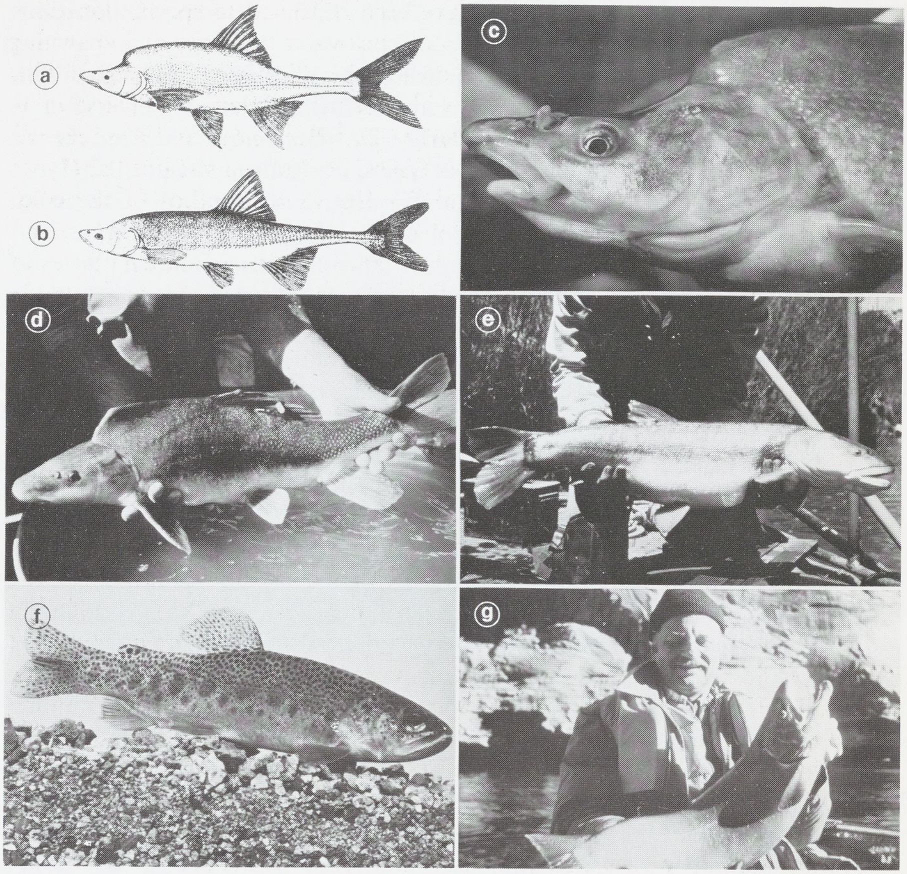

Plate 1. Fish of the Colorado system: (a) *Gila cypha*, (b) *Gila elegans*, (c) *Gila cypha*, showing nuchal hump, (d) *Xyrauchen texanus*, (e) *Ptychocheilus lucius*, (f) *Salmo gilae* and (g) *Salmo gairdneri* from the Lee Ferry fishery. (Photos a, b: Behnke & Benson 1980; c, d, e: R. Valdez; f: U.S. Forest Service; g: Arizona Game & Fish Dept).

The reproductive habits of the rare big-river fish are gradually being documented (Miller *et al.* 1982), as surviving populations are discovered (see Stanford & Ward 1986a: Fig. 1). It appears that all are spring spawners, responding to the warmer spring runoff. Both minnows and suckers move into small streams to spawn. The squawfish migration was spectacular before regulation, with many large, light-coloured spawners (hence "white salmon"). Stanford (unpublished) has observed pre-regulation runs of squawfish and roundtail chub in tributaries of the lower Gunnison River. The longheld view that these fish moved great distances from the mainstream to spawn is challenged by the limited movement of radio-tagged spawners in the Yampa River (Tyus *et al.* 1982). Some populations may have been restricted to specific locations because habitats combining suitable food, backwater nurseries and spawning sites were limited. This could have been an additional isolating mechanism that, with the great age of the Colorado River, may help explain the diverse morphologies of the big-river fish, particularly *Gila, Rhinichthys* and *Catostomus.*

The ecology of the headwater fauna is typical of rhithron streams (cf. Hynes 1970). Ward *et al.* (1986) described the productive zoobenthos of the cold, Upper Basin streams, the major prey of *Cottus, Salmo* and *Rhinichthys*, and Rinne (1980, 1982) described the ecology of native salmonids in tributaries of the Gila. The spinedace (*Lepidomeda vittata*), an endangered species, occurs in most north-flowing tributaries of the upper Little Colorado Basin. These streams often are reduced to pools, yet this remarkable species persists, though not in association with exotic fish (Minckley & Carufel 1967).

Fish in the Virgin and Pluvial White rivers and desert segments of the Gila system are remarkably well-adapted to life in extreme temperatures (35–45°C), high salinities (to *c.* $90\,g\,l^{-1}$) and drought (Deacon & Minckley 1974). During dry periods, the longfin dace (*Agosia chrysogaster*) is able to persist beneath algal mats and debris that are only slightly moist. This fish has a high reproductive capacity, and a few adults may repopulate the stream within a few weeks (Minckley & Barber 1971). The desert pupfish seemingly appears from the sand following wet weather (Minckley 1973), and prefers highly saline habitats like the Salton Sea. However, extreme flooding or prolonged drought may eliminate desert fish from stream segments. Collins *et al.* (1981) reported that an introduced population of the endangered Gila top minnow (*Poeciliopsis occidentalis occidentalis*) was eliminated from one desert stream by flooding. Ephemeral streams, when re-watered, rapidly produce plant material (Busch & Fisher 1981; Fisher *et al.* 1982), providing a food base for omnivorous fish which in turn can reproduce rapidly to ensure survival through the succeeding dry period. On the other hand, fish in the desert springs of the Pluvial White River occupy homogeneous, perennial environments. These omnivorous fish use a limited, but reliable food supply, and have developed related adaptations of anatomy and behaviour (Cross 1976; Constantz 1981; Deacon & Minckley 1974).

The fish fauna of the regulated system

The present fauna of the Colorado system is dominated by exotic species (Table 2), except in a few isolated locations (sse Stanford & Ward 1986a: Fig. 1). Of the 32 native freshwater fish listed in Table 1, one is extinct and 15 occur in sparse populations. In the headwaters of the Upper Basin, the range of the Colorado River cut-throat trout (*Salmo clarki pleuriticus*) is limited to two or three isolated populations (Behnke & Benson 1980). Less than 8000 specimens of *S. gila* (Plate 1f) remain in its native habitat in the upper Gila Basin,

Table 2. Fish introduced to the Colorado system, but including only those established as reproductive populations (after Minckley 1973, 1979; Lee *et al.* 1980, and an unpublished compilation by Dr R. J. Behnke, Colorado State Univ.). Hybrids, subspecies and marine species introduced to the Salton Sea are not considered. Distributions are rare (R), common (C) or abundant (A) in the Upper (U) and Lower (L) Basins. Preferred habitats in parentheses are reservoirs (R), lakes (L), streams (S) or desert springs (Sp).

FAMILY species	Common name	Distribution	Habitat
CLUPEIDAE			
Dorosoma petenense (Günther)	Threadfin shad	A, L and Lake Powell	(R)
SALMONIDAE			
Oncorhynchus kisutch (Walbaum)	Coho salmon	R, U	(R)
Oncorhynchus nerka (Walbaum)	Kokanee (red salmon)	R, L; C, U	(R, S)
Salmo gairdneri Richardson	Rainbow trout	C, L; A, U	(R, L, S)
Salmo trutta Linnaeus	Brown trout	C, L; A, U	(R, L, S)
Salvelinus fontinalis (Mitchell)	Brook trout	C, L; C, U	(R, L, S)
Salvelinus namaycush (Walbaum)	Lake trout	C, U	(R, L)
Thymallus arcticus (Pallus)	Arctic grayling	R, U	(L)
ESOCIDAE			
Esox lucius Linnaeus	Northern pike	R, U	(R, S)
CYPRINIDAE			
Carassius auratus Linnaeus	Goldfish	C, L	(R, S)
Couesius plumbeus (Agassiz)	Lake chub	R, U	(S)
Cyprinus carpio Linnaeus	Carp	A, L; A, U	(R, L, S)
Gila atraria (Girard)	Utah chub	C, U	(R, S)
Gila copei (Jordon & Gilbert)	Leatherside chub	R, U	(R, S)
Notenigonus crysoleucas (Mitchell)	Golden shiner	C, L	(R, S)
Notropis lutrensis (Baird & Girard)	Red shiner	C, L; R, U	(R, S)

Table 2. (continued)

FAMILY species	Common name	Distribution	Habitat
Notropis stramineus (Cope)	Sand shiner	R, L; C, U	(R, S)
Pimephales promelas Rafinesque	Fathead minnow	A, L; A, U	(R, S)
Rhinichthys cataractae (Valenciennes)	Longnose dace	R, U	(S)
Richardsonius balteatus (Richardson)	Redside shiner	C, U	(R, L, S)
Semotilus atromaculatus (Mitchell)	Creek chub	R, U	(S)
CATOSTOMIDAE			
Catostomus ardens (Jordan & Gilbert)	Utah sucker	R, U	(S)
Catostomus catostomus (Forester)	Longnose sucker	R, U	(R, S)
Catostomus commersoni (Lacépéde)	White sucker	R, L; C, U	(R, L, S)
ICTALURIDAE			
Ictalurus melas (Rafinesque)	Black bullhead	R, L; C, U	(R, L, S)
Ictalurus natalis (Lesueur)	Yellow bullhead	C, L	(R, S)
Ictalurus punctatus (Rafinesque)	Channel catfish	A, L; A, U	(R, S)
Pylodictis olivaris (Rafinesque)	Flathead catfish	C, L	(R, S)
CYPRINODONTIDAE			
Fundulus zebrinus Jordan & Gilbert	Plains killifish	C, U & Grand Canyon	(S)
POECILIIDAE			
Gambusia affinis (Baird & Girard)	Mosquitofish	A, L; R, U	(R, L, S)
Poecilia latipinna (Lesueur)	Sailfin molly	A, L	(R, S)
Poecilia reticulata Peters	Guppy	R, L	(S, Sp)
Poecilia "sphenops" complex	Shortfin (Mexican) molly	C, L	(R, S, Sp)
Xiphophorus maculatus (Günther)	Southern platyfish	R, L	(Sp)

Table 2. (continued)

FAMILY species	Common name	Distribution	Habitat
PERCICHTHYIDAE			
Morone chrysops (Rafinesque)	White bass	R, L; R, U	(R)
Morone mississippiensis Jordan & Eigenmann	Yellow bass	R, L	(R)
Morone saxatilis (Walbaum)	Striped bass	A, L; C, U	(R, S)
CENTRARCHIDAE			
Lepomis cyanellus Rafinesque	Green sunfish	A, L; C, U	(R, L, S)
Lepomis gulosus (Cuvier)	Warmouth	C, L	(R, S)
Lepomis macrochirus (Rafinesque)	Bluegill	A, L; A, U	(R, L, S)
Lepomis microlophus (Günther)	Redear sunfish	A, L	(R, S)
Micropterus dolomieui Lacépéde	Smallmouth bass	C, L; R, U	(R, S)
Micropterus salmoides (Lacépéde)	Largemouth bass	A, L; C, U	(R, L, S)
Pomoxis annularis Rafinesque	White crappie	R, L; R, U	(R, S)
Pomoxis nigromaculatus (Lesueur)	Black crappie	C, L; R, U	(R, S)
PERCIDAE			
Etheostoma exile (Girard)	Iowa darter	R, U	(R)
Etheostoma nigrum Rafinesque	Johnny darter	R, U	(R)
Perca flavescens (Mitchell)	Yellow perch	R, L; R, U	(R, S)
Stizostedion vitreum (Mitchell)	Walleye	C, L; R, U	(R, S)
CICHLIDAE			
Cichlasoma nigrofasciatum (Günther)	Convict cichlid	R, L	(Sp, S)
Cichlasoma severum (Heckel)	Banded cichlid	R, L	(Sp)
Oreochromis mossambicus (Peters)	Moçambique tilapia	A, L	(R, S)
Tilapia zilli (Gervais)	Redbelly tilapia	C, L	(R, S)

and the species is gone from the Verde River (Mello & Turner 1980). The status of Arizona trout (*S. apache*) also is of concern, and nearly all the endemic desert-stream fish are in severe decline (Miller & Lowe 1977). The only viable population of the desert pupfish, once the most common fish in the Southwest, may be an undescribed subspecies isolated in Quitobaquito Spring in Organ Pipe Cactus National Monument, Arizona (Kynard & Garrett 1976; Deacon *et al.* 1979). Except for the speckled dace, the big-river fish have been extirpated from the lower mainstream (Minckley 1979), and humpback chub, speckled dace, bluehead, flannelmouth and perhaps razorback suckers are the only endemics extant in the Grand Canyon (Carothers & Minckley 1981; Carothers & Johnson 1983). Razorback suckers are established and common in Lake Mohave; bonytail chub are also present, but apparently not reproducing (Dr L. Paulson, Univ. Nevada at Las Vegas, pers. commun.). Dams in the Upper Basin have eliminated or adversely affected the native fish for long distances downstream (cf. Vanicek *et al.* 1970; Holden 1979; Stanford & Ward 1984). Only a few isolated canyon habitats (e.g. Yampa River Canyon: Vanicek *et al.* 1970) or unregulated tributaries (e.g. White River: Lanigan & Berry 1981) contain an assemblage of native fish like the pristine river fauna (Table 1). All the native big-river fish, except speckled dace and flannelmouth sucker, face extinction (Tyus *et al.* 1982).

The major causes of the decline relate to loss of riverine habitat and interactions with exotic species. More than one-quarter of the river has been converted to lentic habitats by impoundment (Bishop & Porcella 1980). Fish adapted for the turbid habitats of the main river have not survived in reservoirs, with the possible exception of razorback suckers (Kimsey 1957; Minckley 1979; Holden & Wick 1982). Regulated flows have armoured the river bottom in tailwaters, and most of the crucial backwaters and marshes no longer receive water. The thermal régime and trophic structure of remaining river segments have been changed by releases from reservoirs. Diversions and pumping of groundwaters have dried out many desert streams (e.g. lower Gila River: cf. Holden 1979) and springs (Naiman 1981). However, Minckley (1979) points out that even these abrupt changes are no more severe, and perhaps are less general, than climatic changes which have occurred in the recent history of the basin: since the Pliocene, most of the native fauna has endured successive pluvial episodes followed by desertification. But at no time were the native fish confronted with numerous introductions of highly competitive, exotic species, some carrying alien diseases (cf. Holden 1979; Holden & Wick 1982; Deacon 1979; Carothers & Minckley 1981). Presently more than 50 exotic fish, led by carp (*Cyprinus carpio*), threadfin shad (*Dorosoma petenense*), rainbow trout (*Salmo gairdneri*) and largemouth bass (*Micropterus salmoides*), are established in the basin (Table 2). Others have been introduced but apparently are not reproducing (Minckley 1973, 1979; Moyle 1976; Nicola 1979; Courtnay & Deacon 1983). Exotic species prey on the eggs and juveniles of indigenous fish, and compete for space and spawning sites (Deacon 1979). Thus, red shiners (*Notropis lutrensis*) have replaced the Gila spinedace (*Meda fulgida*), and exotic mosquitofish (*Gambusia affinis*) have replaced the Gila topminnow (*Poeciliopsis occidentalis occidentalis*) in the Gila drainage. Mosquitofish also have replaced desert pupfish in the Salton Sea, and exotic largemouth bass (*Micropterus salmoides*) and sailfin mollies (*Poecilia latipinna*) have replaced Moapa dace (*Moapa coriacea*) and White River springfish (*Crenichthys baileyi*) (Minckley & Deacon 1968; Minckley 1973; Deacon 1979). Minckley (1979) believes that the greatest impact is in predation on juvenile natives, especially by juvenile exotics. In some cases, hybridisation between native and exotic species has "swamped" the native gene pool (e.g. rainbow X cut-throat trout: Behnke & Benson 1980). Further, range restrictions and habitat changes, including the effects of exotic species, may be enhanced by hybridisation between native species (e.g. razorback X flannelmouth sucker: Hubbs & Miller 1953; Tyus *et al.* 1982).

Exotics have been especially successful in reservoirs (Stanford & Ward 1986b) and closely regulated segments (Stanford & Ward 1986a: Fig. 1). The major fisheries in Lower Basin reservoirs involve the planktivorous threadfin shad, which provides food for largemouth (*Micropterus salmoides*) and striped bass (*Morone saxatilis*) (Dill 1944; Kimsey 1957; Minckley 1973). In Upper Basin reservoirs a host of introduced suckers, minnows and trout are present. Throughout the system, introduced fish have become established in the remaining river segments through stocking or migration from the reservoirs (Table 2).

The Serial Discontinuity Concept of Ward & Stanford (1983) – the idea that regulated rivers tend to ecologically reset or mimic upstream or downstream lotic conditions – predicts that native species should be re-established some distance downstream from a dam. However, in the Colorado system there may no longer be sufficient river lengths for this to occur, especially with the presence of the exotic species. Big-river endemic species survive in the lower Green River and the mainstem above Lake Powell because conditions approach pre-regulation conditions, but even these segments are likely to be affected by dams proposed or under construction on the lower reaches of the Yampa, White, Dolores and Gunnison rivers.

Productive exotic sport fisheries have been created below several dams: growth rates of trout reportedly are more than 38–40 cm annually (Wiley & Duffer 1980). Some fisheries have developed immediately below dams (e.g. Lee Ferry fishery below Glen Canyon Dam), and others (e.g. lower Gunnison River) are most productive some distance downstream from the dam, as cold temperatures in the tailwaters are ameliorated by warm air temperatures and side flows (Stanford & Ward 1983, 1984).

A productive fishery developed in the Green River below Flaming Gorge Dam as the reservoir was filling (1962–68), but declined dramatically in response to cold (4°C) releases after the reservoir filled (maximum depth 134 m). In an effort to salvage the fishery in 1978 the dam was fitted with multi-level release gates to allow a constant summer tailwater temperature of *c.* 13° C. Trout growth increased 3–4 fold in the warmer water (Larson *et al.* 1980).

The Lee Ferry fishery below Lake Powell involves a simple food chain, and produces fast-growing rainbow and other introduced trout (Plate 1g). The clear, nutrient-laden water from the hypolimnion of Lake Powell stimulates growths of the green alga *Cladophora glomerata* on the river bottom, sustaining high production of introduced amphipods (*Gammarus lacustris*; see Ward *et al.* 1986), in turn fed upon by trout. This fishery extends well into the Grand Canyon and is a very different trophic system to the one that existed before impoundment.

Conclusion

The indigenous fish of the Colorado system have few marine affinities (Miller 1958) and are 85% endemic (66% at the species level), suggesting long isolation. For some forms, however, survival may depend on artificial propagation (Greger & Deacon 1982; Hammon & Inslee 1982). The system now is so altered by regulation that questions about ecology of fish in the virgin river are largely academic. Non-native species abound throughout, and the prospect for further introductions is strong. Populations will likely fluctuate widely as interspecific competition and the ecological consequences of regulation differentiate "winners and losers".

Many research opportunities remain. Relationships between processes in reservoirs and tailwaters and successful fish populations are little understood. The life histories and needs of forage organisms and factors controlling primary productivity must be related to the fish communities, especially if sport species are to be preferred. The regulated Colorado system provides experimental macrocosms in which organism-level (e.g. gene expression) or ecosystem-level (e.g. reservoir influences) theories may be tested (cf. Ward & Stanford 1984). Answers to these questions may help to couple the benefits of regulation with the natural attributes of the system.

Acknowledgements

We thank Dr R. Behnke and G. Wilde for reviewing the manuscript and R. Valdez, J. Rinne, W. Dreyer, J. Johnson, C. Carlson, R. Harris and G. Bryant for unpublished material.

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9C. Lotic zoobenthos of the Colorado system

J. V. Ward, H. J. Zimmermann & L. D. Cline

Introduction

The Colorado River System provides a diverse array of habitats for lotic zoobenthos, reflecting the extreme ranges of climate, vegetation, and geology within the basin (Stanford & Ward 1986). Running-water habitats vary from cool, clear, forested headwater reaches traversing crystalline bedrock at high elevations, to warm, sluggish, silt- and salt-laden river reaches in desert areas near sea level. However, clear, cold reaches occur in desert regions in tailwaters below high dams, and low-altitude headwaters may be warm and saline with low gradients and fine substrata.

This chapter is a first attempt to provide an ecological perspective of the benthic macroinvertebrates of the Colorado system. Few papers in scientific journals have dealt specifically with lotic zoobenthos, especially of the Lower Basin, although some data exist in reports of government agencies and consulting firms. Information for the Lower Basin, frequently based on pre- or post-impoundment studies, is primarily in technical reports or mimeographed materials; such sources are only selectively drawn upon here. Most data for the Upper Basin are from studies in the laboratory of the senior author.

The chapter is in three sections. The first reviews data on zoobenthos at several mainstem locations (i.e. Colorado River proper), from a headwater site in the Rocky Mountains (Colorado) to the lower reaches (Arizona). The second describes the communities at selected tributary sites, from headwater to riverine habitats. The third section concerns the influence of impoundment on downstream benthic communities. No attempt is made to assess other anthropogenic changes such as mining, grazing or organic pollution, and only limited data on environmental conditions are presented (see Stanford & Ward 1986).

Sample locations (Fig. 1) have been grouped into three categories according to the terminology of Illies & Botosaneanu (1963). This provides a general idea of the character of the running water habitat: the *crenon* and *upper rhithron* include spring sources, springbrooks and other headwater streams (cf. stream

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order *c.* 1–3), the *middle* and *lower rhithron* corresponds to middle reaches (stream order *c.* 4–6), and the *potamon* includes rivers (stream order *c.* 7 or more). The crenon and upper rhithron sites (Fig. 2) occupy the widest range of elevations, and the middle and lower rhithron segments, all in the Upper Basin, occupy the least range.

Colorado River mainstem

Eight mainstem sites (A–H: Fig. 1) are examined here. Site A is a first-order segment at the very headwaters of the Colorado River, a subalpine meadow (3105 m) in northern Colorado. At site B, near Granby, Colorado, the river is in the middle/lower rhithron category, and the remainder (C–H) are potamon environments. Except at the headwater site, all are influenced by stream regulation (Ward & Stanford 1979), although pre-impoundment data are available for some. Except for studies in reservoir tailwaters, zoobenthos data for mainstem locations are primarily qualitative.

Site A samples were taken several hundred metres downstream from the river source, after the water had formed a distinct channel. Samples were also collected from a nearby first-order tributary (Bennett Creek: site 1; 3108 m). Each locality has soft water, a steep gradient, rubble and boulder substratum and an extended 7-month period of ice and snow cover. The fauna includes cold stenotherms and some eurythermal species. Five orders of insects (Ephemeroptera, Plecoptera, Trichoptera, Diptera and Coleoptera) contributed over 97% of the total zoobenthos at each location, as is typical of high-altitude streams in this region (Short & Ward 1980a). The elmid *Heterlimnius corpulentus* is the only beetle present. Winter stoneflies emerge as openings appear in the ice (late May, early June); adult *Zapada*, *Capnia*, *Paraleuctra* and *Taenionema* may be found crawling along the snow-covered stream banks. *Baetis bicaudatus* and several heptageniids are the predominant mayflies. The trichopteran fauna is dominated by cohabiting species of *Rhyacophila*, and chironomids, tipulids and empidids are the most abundant dipterans. The turbellarian *Polycelis coronata* is the most common non-insect, although oligochaetes, nematodes and water mites are also present. These subalpine sites support a more diverse zoobenthos than streams above the tree line (cf. Allan 1975; Ward 1982).

Data for *site B* (Stanford & Ward 1986: Plate 1a) prior to regulation (Weber 1959) are markedly different to those for the headwater site. Although a few species had dropped out, major groups were added, including leeches, snails and several families of insects (e.g. pteronarcid stoneflies, hydropsychid and brachycentrid caddisflies).

At *site C*, above Glenwood Canyon, Colorado, the river is a potamon environment. It carries a heavy silt load, although rocky areas occur. Odonates are present, but plecopterans are less abundant and diverse than upstream. The

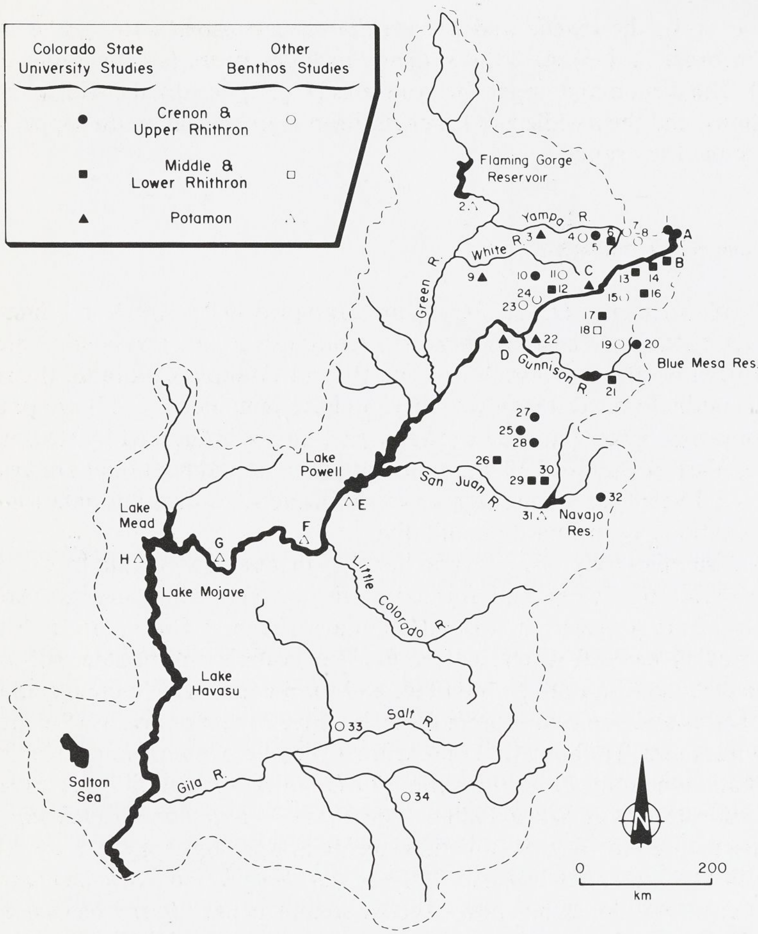

Figure 1. The Colorado Basin, showing some major reservoirs. The mainstem is shown as a heavy line, the major tributaries as lighter lines. Sample locations are indicated by letters (mainstem) or numerals (tributaries); each represents one or more sites. Where data are available from the research laboratory of the senior author, studies conducted by other investigators in that vicinity are not indicated. Not all sites on the map are specifically addressed in the text, especially if only qualitative data exist.

riverine mayfly *Traverella albertana* occurs, but heptageniid mayflies, so diverse and common in the rhithron, are limited to the warm-adapted *Heptagenia*. Other typical members of the rhithron fauna, including rhyacophilid caddisflies, the turbellarian *Polycelis coronata* and blephariceridś, are absent.

Site D is near the Utah border in Colorado. Stoneflies are rare, but amphipods, megalopterans and crayfish are present, and the mayflies *Traverella albertana* and *Baetis* spp. are abundant. Burrowing mayflies (Ephemeridae,

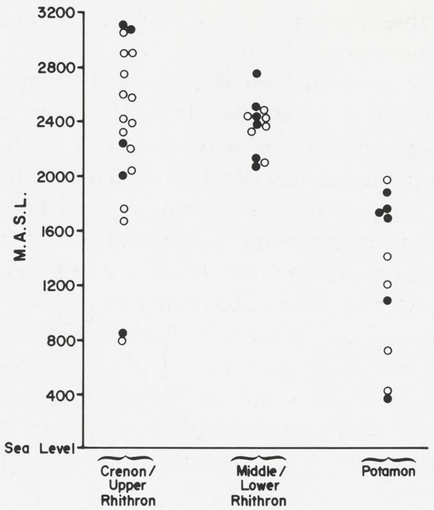

Figure 2. Altitudinal distribution of lotic sites referred to in this chapter. Each circle represents one or more stations; solid circles are the locations in Table 2.

Polymitarcyidae) occur in habitats (e.g. the Green, White and Yampa rivers) comparable to sites C and D, although we have no confirmed records for those areas. The riverine naucorid bug *Ambrysus mormon* and several families of beetles (e.g. Dytiscidae, Hydrophilidae) probably also occur. The limited samples, difficulties of collecting burrowing mayflies, and the mobility of hemipterans and coleopterans may explain their apparent absence. Despite seemingly suitable habitat conditions, freshwater mussels do not occur in the Colorado River Basin within the State of Colorado (Brandauer & Wu 1978).

Prior to construction of Lake Powell (Utah-Arizona), the Glen Canyon reach of the Colorado River (*site E*) was a swift, turbid, warm but well-oxygenated river, with a bottom of mostly shifting sand (Dibble 1959). Algae and invertebrates occurred on rocks or wood debris above the sand, or on the downstream sides of rock faces. Dibble's (1959) samples from sand habitats did not yield a single macroinvertebrate, although the sand-dwelling mayfly *Homoeoneuria* occurred in a tributary. A diverse aquatic insect fauna (over 91 species) was collected, mainly from the tributaries, and most specimens collected from the main river occurred at the mouth of tributaries. For example, none of 22 recorded beetle species was found in the main river. Eighteen zoobenthic species were taken from the Colorado proper. The predominant mayflies were *Traverella albertana* and *Heptagenia elegantula*, with a few specimens of the oligoneuriid *Lachlania powelli*. *Potamyia*, the predominant caddisfly in the Colorado River, was not collected from the tributaries. Three odonates, several dipterans and the megalopteran *Corydalus* also occurred in the river proper.

Plecopterans were absent from all sites. Apparently no attempt was made to collect non-insect macroinvertebrates.

Before construction of Glen Canyon Dam, water temperatures in the Grand Canyon (*site F*; Stanford & Ward 1986: Plate 1d) approached 30°C in summer, but fell nearly to freezing in winter (Cole & Kubly 1976). As in Glen Canyon, severe floods and high silt- and bed-loads provided poor habitat for zoobenthos. The tributaries again appear to be important in supplying organic detritus to the mainstem river, and in maintaining the populations of river benthos.

Data on zoobenthos of the Colorado River in the Grand Canyon are extremely sparse; virtually none exist prior to construction of Glen Canyon Dam 123 km upstream (1963). Amphipods (*Gammarus lacustris*) were introduced as fish-food in 1932 and 1965; the latter introduction also included unidentified snails, leeches, caddisflies, damselflies and mayflies (Table 1). Only Cole & Kubly (1976) and Carothers & Minckley (1981) have systematically sampled aquatic macroinvertebrates, and both studies concentrated on tributaries rather than the mainstem.

Cole & Kubly (1976) collected amphipods, oligochaetes, water mites, chironomids, ceratopogonids and the snails *Physa* and *Lymnaea* from the mainstem in the Grand Canyon. They found a striking difference between the zoobenthos of tributaries and that of the mainstem, with most species occurring only at tributary sites. Only three groups (oligochaetes, chironomids and gastropods) exhibited significant overlap between mainstem and tributary habitats. With the exception of amphipods, which were confined to the mainstem, it appears that the zoobenthos of the Colorado River consists primarily of the few tributary species able to tolerate riverine conditions.

Carothers & Minckley (1981) collected amphipods, physid snails, oligochaetes, corixid bugs and simuliids at mainstem locations during 1977–78. Again, major groups of insects present in the tributaries (mayflies, stoneflies, caddisflies, beetles, dragonflies, dobsonflies and aquatic moths) were not found in the river proper. Densities for the Colorado River in the Grand Canyon ranged from 5–20 organisms m^{-2}.

From recent limited sampling, there is no evidence that a specially-adapted riverine zoobenthos ever resided in the river mainstem. The tremendous silt loads, extreme fluctuations in discharge and high current velocities (to $5\,m\,s^{-1}$) may have prevented development of a diverse and abundant zoobenthos. If a well-adapted lotic invertebrate fauna did exist, either it has been extirpated by man's modification of the environment (see Cole & Kubly 1976; Dolan *et al.* 1974; Stanford & Ward 1986), or it has eluded detection because of inaccessibility and sampling difficulties.

There are no data for the river segment inundated by Lake Mead (construction of Hoover Dam began in 1931), but in 1978–79 McCall (undated) sampled benthos at four locations upstream from the reservoir (*site* G). Collections consisted primarily of low numbers of chironomids and simuliids, with

Table 1. Zoobenthos introduced to the lower Colorado River (sources cited in text)

Taxon	Introduced	Recent distribution
Gammarus lacustris	Bright Angel Ck 1932 Below Hoover Dam 1941, 1972 Lee Ferry 1965	Glen Canyon Dam tailwater Grand Canyon (mainstem) Mainstem above L. Mead Hoover Dam tailwater L. Mojave tailwater
Palaemonetes paludosus	L. Havasu 1958, 1962, 1963 Below Parker Dam 1963 Alligator Slough 1963 Palo Verde 1963	Davis Dam downstream
Crayfish[a]	Bait releases 1930s, 1940s Winterhaven 1935 Picacho 1941	Widespread, river and reservoirs
Corbicula fluminea	Unknown source 1940s	L. Mead downstream, river and reservoirs
Lymnaeidae[a] prob. *Lymnaea*	Lee Ferry 1965	Widespread, river and reservoirs
Physidae[a] prob. *Physa*	Lee Ferry 1965	Widespread, river and reservoirs
Hirudinea[a]	Lee Ferry 1965	Glen Canyon tailwater downstream
Zygoptera (Odonata)[a]	Lee Ferry 1965	Widespread, primarily reservoirs, backwaters, tributaries
Ephemeroptera[a]	Lee Ferry 1965	Widespread, some abundant in tailwaters
Trichoptera[a,b]	Lee Ferry 1965	Widespread, river and reservoirs

[a] Indistinguishable from indigenous populations without knowing precisely which species were introduced.
[b] Hydroptilids and hydropsychids may be abundant in tailwaters.

nemourid stoneflies, dytiscid beetles and libellulid dragonflies also present. Amphipods were observed in the river, but did not occur in benthic samples. Mean densities of total zoobenthos were extremely low, never exceeding one organism m^{-2}. The riverine habitat in Black Canyon (*site H*) below Hoover Dam has been severely changed by stream regulation (see later).

The remainder of the lower river flows through low-lying desert terrain to the sea. The few data on zoobenthos have been summarised and documented by the United States Fish & Wildlife Service (1981). Prior to dam construction in this region, suspended solids at times exceeded 30 000 $mg\,l^{-1}$ and mainstream water temperatures reached 32°C. Although pre-impoundment studies are not available, this section of the river probably was very unproductive with chironomids and oligochaetes as dominant benthic organisms. Lake Mojave, formed by Davis Dam, is the lowermost impoundment to support a cold-water tailrace trout fishery; the others are shallow and do not greatly affect downstream temperatures, although clear-water releases and seston do produce special habitat conditions immediately below the dams (Minckley 1979).

In addition to oligochaetes and chironomids, common animals in the lower river include gastropods, leeches, turbellarians, sphaeriid clams, odonates, beetles, simuliids, net-spinning caddisflies and baetid mayflies. The introduced Asiatic clam (*Corbicula fluminea*) became established in the 1940s and presently occurs at least as far upstream as Lake Mead (Table 1). Freshwater shrimp (*Palaemonetes paludosus*), crayfish, snails and gammarid amphipods have been introduced as fish food. The shrimp, crayfish and molluscs are locally abundant, but the amphipods are restricted to reaches like the Grand Canyon and Black Canyon, where summer temperatures are depressed by deep-release dams.

There appear to be no major groups of zoobenthos indigenous to the Lower Basin that do not occur also in potamon reaches of the Upper Basin. It is curious that freshwater mussels are virtually absent from the entire Colorado River Basin (Bequaert & Miller 1973; Brandauer & Wu 1978), considering that North America has a rich unionacean fauna.

Colorado River tributaries

Data for 34 tributary locations are considered (Fig. 1): 18 crenon-upper rhithron sites, 11 middle-lower rhithron sites and 5 potamon sites. For some, however, the information is limited or merely qualitative; only those for which relatively comprehensive data exist are considered (cf. Table 2). Some information is from unpublished studies from the laboratory of the senior author.

Data for five crenon–upper rhithron sites are presented in Table 2. Site A, at the headwaters of the Colorado, and nearby Bennett Creek (site 1) are included despite a limited data base, because these are the only high-elevation sites for which quantitative data exist [Allan's (1975) excellent work on Cement Creek (site 19) is incompatible with our data]. A two-year study of Trout Creek (site 5) has been conducted to assess the effects of coal-mine drainage on the zoobenthos (Ward *et al.* 1978; Canton & Ward 1981); only data from unimpacted stations are considered here. Four years' data are available for Piceance Creek and tributaries in the cool-desert Upper Basin (site 10; see Gray *et al.* 1983); zoobenthos from springs and springbrooks of this system will be compared with Aravaipa Creek in the Lower Basin Sonoran Desert (site 34: Bruns & Minckley 1980).

Sampling was conducted in six middle-lower rhithron habitats (Table 2), each a reference site for regulated stream studies (map codes in Table 2 correspond to sites in Fig. 1). Annual studies have been completed on the Yampa, Williams Fork, and Blue rivers, and seasonal data have been obtained for the Fryingpan

Table 2. Mean density and Shannon diversity for lotic zoobenthic communities at selected locations in the Colorado Basin. Data for regulated (REG) and reference (REF) sites are given if available. Regulated sites are in the tailwaters below deep-release dams; reference sites are unregulated lotic segments. Reference sites which serve as "controls" for tailwater sites generally are upstream from the reservoir, although at site B a tributary (Fraser R) and at site 2 a downstream station (Echo Park) served as reference locations.

Stream (map code)	Elevation (m)	Organisms m^{-2}		Shannon Index		Source
		REF	REG	REF	REG	
Crenon/upper rhithron						
Colorado R (A)	3058	696	–	3.7	–	Unpublished
Bennett Ck (1)	3108	1648	–	3.3	–	Unpublished
Trout Ck (5)	2241	2751	–	3.3	–	Ward *et al.* 1978
Piceance Ck (10)	2000	19 700	–	3.2	–	Gray *et al.* 1983
Aravaipa Ck (34)	835	12 240	–	3.3	–	Bruns & Minckley 1980
Middle/lower rhithron						
Colorado R (B)	2521	7664	17 757	4.4	2.1	Unpublished[b]
Yampa R (6)	2072	1160	21 718	4.2	1.5	Unpublished[b]
Rifle Ck (12)	2133	2295	2292	3.5	3.2	Unpublished
Williams Fork (13)	2438	813	2294	4.2	3.0	Unpublished[b]
Blue R (16)	2748	7450	11 631	4.5	3.1	Unpublished[b]
Fryingpan R (17)	2367	4204	18 182	4.1	2.7	Unpublished
Potamon						
Green R (2)	1710	2238	25 144	3.0	1.9	Pearson *et al.* 1968
Yampa R (3)	1828	(968)[a]	–	3.0	–	Ames 1977
White R (9)	1661	(972)[a]	–	2.6	–	Ames 1977
San Juan R (31)	1740	–	4927	–	1.3	Graves & Haines 1969
Colorado R (E)	1082	–	775	–	1.1	T. McCall pers. commun.[b]
Colorado (H)	372	–	373	–	1.8	Paulson *et al.* undated

[a] Means per one-minute kick samples.
[b] Based on a partial data set.

and Fraser rivers (reference for site B) and Rifle Creek. All are rubble-bottomed trout streams at middle elevations in the Rocky Mountains.

Comprehensive data are available for only three unregulated potamon segments, all in the Upper Basin (Table 2). Ames (1977) took year-round semi-quantitative samples of insects in the White and Yampa rivers, Colorado. The Echo Park site of Pearson *et al.* (1968) on the Green River, Utah, is 106 km below Flaming Gorge Reservoir, where the effects of regulation are no longer apparent. At other potamon sites in Table 2, quantitative data are available only for tailwaters. Except for the two lower river sites, the potamon sites are at elevations where winter water temperatures approach freezing.

Composition and abundance

Pennak (1977) surveyed Rocky Mountain trout streams, 13 in the Upper Basin. The locations of eight of these streams are shown in Fig. 1 (sites 4, 7–8, 11, 15–16, 23–24). Mean zoobenthos densities at 14 sites (1552–2805 m elevation) on the eight streams ranged from 149–1450, with a grand mean of 639 organisms m^{-2}. Biomass (wet weight) means ranged from 1.3–8.3, with a grand mean of 4.7 $g\,m^{-2}$. These low figures reflect the unproductive nature of steep mountain streams.

Densities in Table 2 generally are higher than those reported by Pennak. Excluding regulated sites (considered later), lowest values were in the headwaters of the Colorado River, and highest values in the crenon habitats of Piceance Creek, a cool-desert stream, and Aravaipa Creek, a hot-desert stream. In Sycamore Creek (site 33), another Sonoran Desert stream in Arizona, Gray (1981) found extremely rapid development (1–3 weeks from egg to adult) and continuous reproduction of mayflies, chironomids and a corixid species. The mean annual density of total zoobenthos was *c.* 80 000 organisms m^{-2}.

Species diversities (Shannon & Weaver 1963) at unregulated sites were in the range expected for macroinvertebrate communities of unpolluted streams (cf. Wilhm 1970). The tendency for higher diversities to occur in middle reaches (Table 2) conforms to the River Continuum Concept (Vannote *et al.* 1980); this is recalled in later discussion.

Ephemeroptera, Trichoptera and Diptera are numerically abundant (each more than 10% of the total fauna) in all unregulated stream reaches (Fig. 3). Two groups, the Plecoptera and Coleoptera, comprise less than 10% of the total zoobenthos in all reaches, and non-insects are common only in crenon-upper rhithron habitats. Mayflies and caddisflies exhibit an increase, and stoneflies and non-insects a decrease in relative abundance from headwaters to potamon sites. Beetles and dipterans each show comparable relative abundances in upper and middle reaches, but decline in potamon sites.

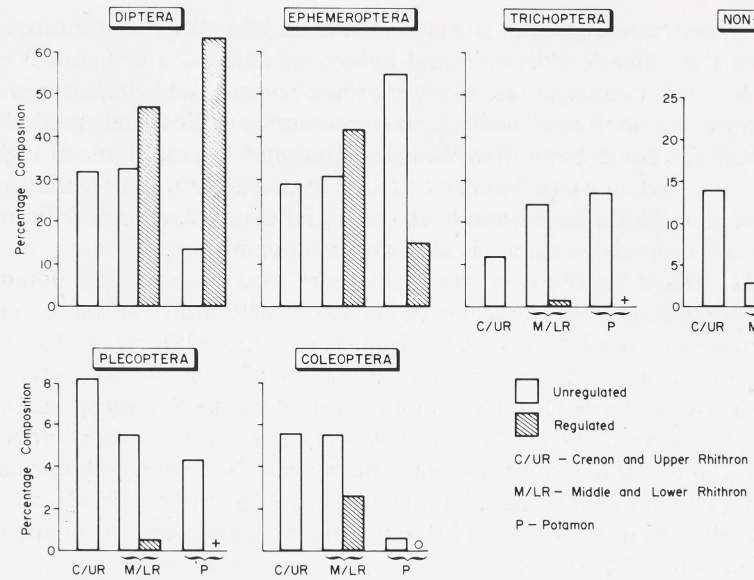

Figure 3. Percentage composition of major taxa based on grand means from locations in Table 2. Values are based on numbers as biomass data are unavailable for some sites. Non-insect data at unregulated potamon sites are from Green River data only as Ames (1977) did not enumerate non-insects. Note the different vertical scales.

The paucity of mayflies in spring sources (Piceance Creek) suppresses the relative importance values of this group in the crenon-upper rhithron category (Fig. 3). Stoneflies exhibited the greatest relative abundance at high elevations (16% at site 1, 14% at site A), and their importance would be enhanced if low values from spring sources and the hot-desert stream were excluded. The relative importance of non-insects in upper reaches is greatly influenced by their abundance (57%) in crenon habitats of the Piceance Creek system. The low values of non-insects in potamon habitats contrast with the Mississippi system, where crayfish, clams, snails, leeches and other non-insect invertebrates are a major part of the riverine fauna.

As mentioned, the zoobenthos of first-order streams at high elevations (sites 1, A) is almost exclusively insects. Insects also comprise over 90% of the zoobenthos in Trout Creek (site 5), a high-gradient third-order stream, where the macroinvertebrate composition was similar to that of higher elevation systems, but with added taxa. Trout Creek has a well-developed trichopteran assemblage, including hydropsychids not found at higher elevations.

In contrast to surface-runoff headwater streams, non-insects predominate in the rheocrene habitats of the Piceance Creek Basin (site 10). *Gammarus lacustris*, *Polycelis coronata*, *Physa* sp., the sphaeriid clam *Pisidium nitidum*, the leech *Helobdella stagnalis*, and oligochaetes are abundant. Mayflies are rare at spring sources, but *Baetis tricaudatus* and *Ephemerella inermis* are abundant in springbrooks. Only two stoneflies, *Isoperla quinquepunctata* and *Amphinemura banksi*, occur at the sources of springs; other nemourids and capniids reside in springbrooks. The elmid beetle *Heterlimnius corpulentus*, characteristic of high elevations, occurred in large numbers at one spring source. The caddisfly *Hesperophylax occidentalis* occurred in all crenon habitats (Martinson & Ward 1982), and chironomids and tipulids also were abundant.

The zoobenthos of Sonoran Desert streams (sites 33–34) is a combination of Neotropical and Nearctic components (Gray 1981), with a diverse and abundant assemblage of hemipterans and coleopterans. Gray (1981) reported 31 species of beetles in eight families and 10 species of bugs in five families (excluding neustonic forms) from Sycamore Creek, Arizona. Several species of dragonflies, the dobsonfly *Corydalus cornutus*, an aquatic moth, and a variety of mayflies, caddisflies and dipterans was also present. Non-insects comprised a significant portion of the fauna (more than 10% in Aravaipa Creek: Bruns & Minckley 1980), and oligochaetes and Hydracarina were abundant. Amphipods were not found in either stream.

The life history attributes of invertebrates in Sonoran Desert streams differ markedly from those of organisms in mesic regions (Gray 1981). They involve adaptive responses to the frequency and unpredictability of droughts and floods, including extremely rapid development, seasonal reproduction, rarity of dormant stages and various behavioural mechanisms.

The zoobenthic communities of the middle and lower rhithron sites have few distinctive features. The fauna is a more diverse assemblage of the insect groups present at upper rhithron sites, plus a few additional species resulting from upstream incursions of certain potamon elements. Groups which may attain maximum diversity and/or abundance in middle reaches include ephemerellid mayflies, *Arctopsyche*, *Lepidostoma* and *Brachycentrus* among the caddisflies, perlid and perlodid stoneflies and orthoclad chironomids. If any species typifies the lower rhithron in the Upper Basin, it is the stonefly *Pteronarcys californica*. Prior to impoundment, the middle Gunnison River (near site 21) was an ideal environment for this species (Knight & Gaufin 1966; Stanford & Ward 1979). However, a well-defined combination of thermal, substratum and food conditions are required for development of large populations, and few suitable reaches remain.

Survey data from the Green River in Wyoming and Utah (site 2), now inundated or regulated by Flaming Gorge Reservoir, suggest that a distinctive potamon habitat with a unique and specially-adapted riverine zoobenthic community did indeed once exist in the Colorado Basin (Dibble 1960; Edmunds 1973). Prior to impoundment, the Green River was well-oxygenated, warm and somewhat turbid, with sand and rock substrata, pools over 4 m deep, and local accumulations of woody debris. Although quantitative pre-impoundment data are not available, a diverse and apparently highly productive zoobenthos occurred in the river, including a mayfly fauna which was "one of the most unusual and interesting ones known to exist in any part of the world" (Edmunds & Musser in Dibble 1960: 122). *Analetris*, a carnivorous siphlonurid, lived in association with sand-dwelling dragonfly nymphs (*Ophiogomphus intricatus*) and chironomids. Sand-dwelling, carnivorous heptageniids (*Pseudiron* and *Anepeorus*) were present, and *Ametropus albrighti* was quite abundant. *Lachlania powelli*, a filter-feeding oligoneuriid, was abundant in deep water, where it clung to sticks and rocks. Nymphs of *Traverella albertana* occurred on rocky bottoms, and many other mayflies, including burrowing ephemerids and polymitarcyids, were present. Several genera and species were originally described from this portion of the Green River system.

Closure of Flaming Gorge Dam in 1962 inundated 145 km of the potamon habitat and altered environmental conditions for at least 100 km downstream (Pearson *et al.* 1968). Although some of the unusual mayflies occur in other rivers, the remarkable zoobenthic community of this section has been lost forever. One can only speculate regarding the lost opportunities for ecological research.

Mayflies comprised 67% and 56% respectively of the zoobenthos in potamon segments of the White and Yampa rivers (Ames 1977), the major tributaries of the Green River. These rivers support an abbreviated assemblage of the specialised mayfly community adapted to the river environment that prevailed prior to closure of Flaming Gorge Dam. Included are the burrowing species *Ephoron album* and *Ephemera simulans* and the leptophlebiids *Choroterpes albiannulata* and *Traverella albertana*. One specimen of *Ametropus*, a few *Lachlania* nymphs and other more common species also were collected by Ames (1977).

Riverine mayflies may have particular substratum (Edmunds *et al.* 1956; Eriksen 1968) and thermal requirements (Britt 1962). For example, *E. album* requires freezing temperatures to stimulate embryonic development, at least 10°C for egg hatching, and several months of warm temperatures for nymphal maturation (Lehmkuhl 1972). Even minor environmental changes may influence the dynamics of such species.

The net-spinners *Hydropsyche* and *Cheumatopsyche* were the predominant caddisflies in Ames' (1977) samples from the White and Yampa rivers. Beetles from several families, corixids and the riverine naucorid bug *Ambrysus mormon* occurred in small numbers.

Functional feeding groups

According to the River Continuum Concept (Vannote *et al.* 1980), the relative importance of macroinvertebrate functional feeding-groups changes along the course of a stream. Shredders, which feed on coarse particulate organic matter

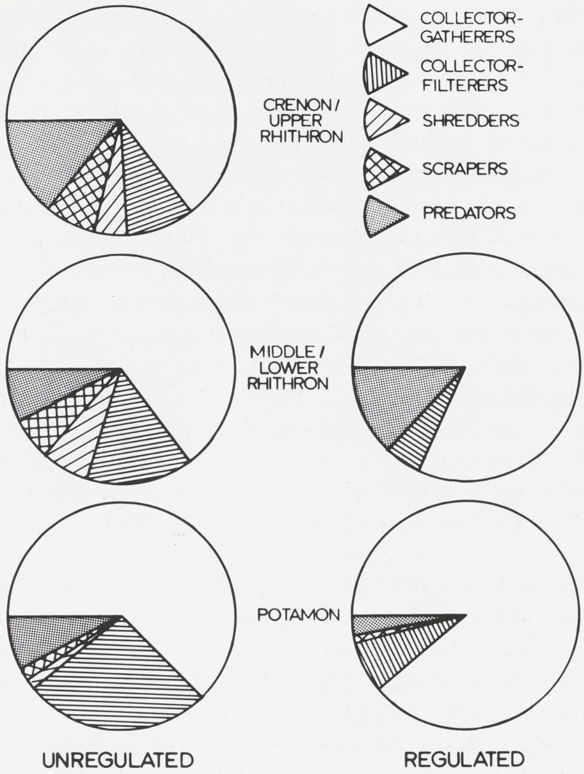

Figure 4. Relative contributions of functional feeding groups based on grand means (numbers) from locations in Table 2. Except where empirical data on food habits are available (Gray & Ward 1979; Martinson *et al.* 1982), trophic assignments are from Merritt & Cummins (1978) for insects and Pennak (1978) for non-insects. Where chironomids were not identified by the investigators, 90% were assumed collector-gatherers and 10% predators. Values less than 1% are not shown.

(CPOM; mainly leaf litter, with particle size greater than 1 mm), supposedly are most abundant in headwaters, and decline downstream as CPOM diminishes in importance relative to other food sources. Collectors, which use fine particulate organic matter (FPOM: less than 1 mm) in transport ('collector-filterers') or as sedimentary detritus ('collector-gatherers'), are abundant in headwaters but comprise 80–90% of the zoobenthos in lower potamon habitats. Scrapers, which graze on attached algae, are most abundant in middle reaches where there is an open canopy and relatively shallow, clear water. Predators are uniformly distributed. These hypotheses were developed mainly for the deciduous forests of eastern North America, where pristine headwater streams are heavily-canopied, light-limited heterotrophic systems receiving large inputs of allochthonous organic matter as leaf litter (but see Minshall 1978).

Data from unregulated sites in the Colorado system (Fig. 4) conform to the model in some respects. Although collectors (gatherers and filter-feeders) are more abundant in headwaters than predicted, the pattern from upper to lower reaches is consistent with the model. The paucity of shredders in upper reaches is expected given the xeric conditions, sparse vegetation and low inputs of CPOM; indeed, this may explain the expanded rôle of collectors in headwater sites. The distribution of predators also conforms generally to the continuum model, but scrapers are less abundant than predicted at middle and lower rhithron sites (Fig. 4). Scouring by spring runoff and spates, and the absence of submerged angiosperms (as attachment sites for algae) may account for the poor development of scrapers in high-gradient streams of xeric regions.

Many characteristics noted by Winterbourn *et al.* (1981) for New Zealand streams apply to streams at middle and high elevations in the Colorado system. In reference to the continuum concept, these authors predict (p. 326) that "rivers arising high in the American Rockies . . . will have ecosystem characteristics essentially like those in New Zealand . . . ". Common features include high gradients, poor detritus retention, sparse deciduous riparian trees, small quantities of woody debris, and an unpredictable physical environment (cf. Ward & Stanford 1983). In New Zealand headwater streams shredders are poorly represented and FPOM is the predominant material ingested by zoobenthos. In both open and forested streams, detritus rather than algae predominates in the diets of most macroinvertebrates. Thus, like Winterbourn *et al.*, we believe that abiotic rather than biotic factors have been of paramount importance in shaping the zoobenthic communities of mountain streams in the Colorado River Basin.

Effects of impoundment on downstream zoobenthos

Dams profoundly alter the structural and functional attributes of downstream zoobenthic communities (Ward & Stanford 1979). With the exception of the headwaters, virtually all running waters in the Colorado Basin are influenced by stream regulation (Stanford & Ward 1986). Here, consideration is given only to locations influenced by deep-release dams, including two potamon sites in the Upper Basin, two potamon sites in the Lower Basin and six rhithron sites in the Upper Basin (Table 2). A major study of the effects of multiple impoundment has been conducted on the Gunnison River system (sites 20–22), but analyses are not yet complete (Stanford & Ward, unpublished).

Despite differences in modes of operation and other variables, streams below deep-release dams share several common features. Long-term fluctuations in discharge are reduced (even below hydro-electric power dams), increasing substratum stability. Clear-water releases create a hydrodynamic disequilibrium, causing erosion of fine particles with an associated increase in mean substratum particle size. The clear waters and stable substrata are an ideal environment for aquatic plants, especially bryophytes and filamentous chlorophytes (Pénaz *et al.* 1968; Lowe 1979).

Dense mats of the green alga *Cladophora glomerata* often cover solid surfaces for several kilometres below dams in the Colorado Basin, and dense beds of angiosperms also may develop in reaches normally devoid of higher plants (Ward 1976a; Holmes & Whitton 1977). In each case the habitat for zoobenthos is affected. Impoundment may also truncate the downstream transport of detritus, affecting the available food resources (Webster *et al.* 1979).

The thermal régime is modified below deep-release dams, with direct and indirect effects on zoobenthos. For example, the annual range of water temperatures in the Grand Canyon prior to impoundment, 0–29.5°C, has been reduced to 6–15°C since the formation of Lake Powell (Cole & Kubly 1976). Species such as *Ephoron album*, which require freezing temperatures to break egg diapause and several months of warm temperatures for nymphal maturation, are unable to complete their life cycles in these conditions.

The result of these and myriad other, more subtle changes in regulated streams is the elimination of many zoobenthic species, the addition of a few, and major shifts in the abundances of taxa able to maintain populations under the altered régime (Ward & Short 1978; Short & Ward 1980b). Species diversity invariably is reduced (Table 2). The effects on total density are variable, but populations of one or more species can attain extremely high levels.

Regulation reduces the relative importance of plecopterans, coleopterans and trichopterans, but enhances that of dipterans (chironomids and sometimes simuliids) and non-insects (amphipods, snails, planarians and oligochaetes) (Fig. 3). The summer-cool and winter-warm environments below deep-release dams, especially where flows are stabilised, are reminiscent of conditions in springbrooks. Indeed, the zoobenthic communities of regulated streams may be quite similar to those of crenon habitats (Ward & Dufford 1979).

Regulation of middle and lower rhithron reaches tends to increase the relative abundance of ephemeropterans (Fig. 3), as increases of *Baetis* spp. more than compensate for the elimination or reduction of other mayflies. In potamon reaches, the overall effect is to reduce the relative contribution of mayflies (Fig. 3), although large populations of *Baetis* occur in Upper Basin tailwaters.

The most complete zoobenthos data for a regulated potamon habitat in the Colorado Basin are those of Pearson *et al.* (1968) for the Green River below Flaming Gorge Dam (site 2). Their Echo Park site was 106 km below the dam, so that effects of regulation were no longer apparent. Thus, it is possible to compare a regulated site 11.7 km below Flaming Gorge Dam with Echo Park (as reference site). *Baetis* sp. 1, chironomids, simuliids and oligochaetes were responsible for the high zoobenthos densities at the regulated site (Table 2). In contrast, a more diverse but less abundant fauna occurred at Echo Park. A reasonably diverse mayfly fauna was present, but with only two of the specially-adapted river species (*Traverella albertana* and *Ephoron album*). *Baetis* sp. 1, common below the dam, was outnumbered only by *Hydropsyche*.

Prior to construction of Navajo Dam, New Mexico (site 31), the San Juan River was a relatively warm and turbid potamon environment (Woodbury 1961). A diverse zoobenthos occurred, including at least 13 species of mayflies, more than six species of stoneflies and caddisflies, the naucorid *Ambrysus mormon*, the dragonfly *Ophiogomphus severus* and numerous dipterans. A trout fishery now exists over at least the first 13 km of the tailwater (Graves & Haines 1969), and seasonal temperatures 1.6 km below the dam range from 5–9°C. The tailwater zoobenthos is composed primarily of chironomids and baetid mayflies, with simuliids and turbellarians also common. Other taxa include lymnaeid, physid and planorbid snails, oligochaetes, leeches, mites, amphipods, and hydropsychid and hydroptilid caddisflies.

As noted earlier, Glen Canyon Dam (site E) has altered conditions in the Colorado River throughout the entire length of the Grand Canyon (site F). In addition to thermal changes, the frequency and severity of floods have been reduced, with hydrodynamic consequences (Dolan *et al.* 1974). An extremely productive trout fishery has developed in the tailwater below the dam, where dense mats of *Cladophora* cover riffle areas (McCall 1981). The data in Table 2 are based on miniponar and Surber samples (collected by SCUBA) at locations over a 24 km stretch below the dam. Four taxa (*Gammarus lacustris*, *Chironomus* sp., *Physa virgata* and oligochaetes) made up essentially the entire benthic fauna (T. C. McCall, Arizona Game & Fish Dept, pers. commun.). The oligochaetes were megadrils, probably the amphibious earthworm *Eiseniella tetraedra*, reported from a regulated segment of the South Platte River (Ward 1976b). A few tubificid oligochaetes were also present. Other zoobenthos seen but rarely collected included nematodes, an unidentified stonefly, simuliids, dytiscid beetles, leeches and the crayfish *Procambarus clarkii*.

The formation of Lake Mead (site H) changed a turbid desert river into a productive trout fishery for at least 40 km downstream from Hoover Dam (Moffett 1942). The tailwater varies little from 12–13°C year-round. Stoneflies were present in collections, though not abundant. *Cladophora* formed a nearly complete mat in riffle areas. Mayflies, especially *Callibaetis*, were abundant, as were hydroptilid caddisflies (with larvae in the algal mats) and chironomids. Dragonfly nymphs and aquatic beetles were collected from trout stomachs. *Gammarus* was introduced in 1941 and became well-established.

When Lake Mojave filled in 1951, impounded water reached upstream nearly to Lake Mead, engendering ecological changes in the Hoover Dam tailwater (Paulson *et al.* undated). Current velocities in the Black Canyon were no longer sufficient to remove the silt introduced by canyon tributaries, and the dense cover of *Cladophora* became restricted to a few kilometres below Hoover Dam. *Gammarus* has been largely replaced by the smaller *Hyalella azteca*. Chironomids (*Chironomus salinarius*, *Cricotopus tremulus*) and *H. azteca* are the predominant zoobenthos immediately below the dam, but are replaced by oligochaetes farther downstream. The snails *Physa* and *Lymnaea*, the turbellarians *Dugesia* and *Phagocata*, and *Hydra* and Hydracarina also occur in the tailwaters. Stoneflies, mayflies and caddisflies have disappeared (Paulson *et al.* undated).

Fig. 4 compares the proportions of functional feeding groups at regulated sites with unregulated (reference) sites. Collectors and predators are essentially the only organisms present in the tailwaters below the deep-release dams. Unlike the situations below surface-release reservoirs (e.g. Ward & Short 1978) or in natural lake outlets (e.g. Illies 1956), where filter-feeders are enhanced, it appears that plankton is not a reliable enough food below deep-release reservoirs to sustain large populations of filter-feeding zoobenthos (Müller 1962; Ward 1975). Apparently the release of lake plankton does not compensate for the reduction of total seston induced by settling in the reservoir. The disruption of detrital transport by the reservoir accounts for the virtual absence of shredders. Scrapers too are poorly represented despite the abundance of algae; this may be merely an apparent anomaly, in that there are so few empirical data on invertebrate feeding habits in regulated streams. Gray & Ward (1979) found that *Cladophora*, the dominant alga at regulated sites, was not extensively utilised as food by zoobenthos, although new growths and decomposing fragments were ingested. The surfaces of living filaments may be colonised by epiphytic diatoms, but the dense growths often eliminate exposed rock surfaces as grazing sites for zoobenthos. Clearly, studies of trophic dynamics among the benthic organisms of tailwaters are a potentially fruitful area for research.

Conclusion

Development of the Colorado system began in earnest during the last century and continues unabated. The demise of the river as a pristine, free-flowing lotic ecosystem was thus assured well before comprehensive ecological studies were contemplated. Introductions of plants and animals further hinder attempts to intellectually reconstruct the river ecosystem. Little evidence is available to suggest the magnitude of direct and indirect effects the exotic biota may have had on the native zoobenthos.

There is no evidence that a highly-adapted riverine zoobenthos, analogous to the endemic fish fauna, ever occurred in the lower Colorado mainstem. However, pre-impoundment studies of mayflies confirm that such a community did exist at potamon sites in the Upper Basin. Alas, only remnants of that remarkable fauna remain.

Some taxa abundant in other rivers in North America and elsewhere are little represented in the Colorado system. Unionacean clams are virtually absent from the entire basin, and isopods typically are absent from lotic sites. It is not clear whether crayfish are indigenous, but despite many introductions flourishing populations of current-adapted species are absent. However, large crayfish populations recently have been discovered in the Gunnison River, in areas of fast current and rocky substrata (Stanford & Ward unpublished).

Although quantitative data indicate some adherence to the River Continuum Concept, it appears that the Colorado system generally lacks the structural and functional integrity of the eastern woodland streams where the concept is largely founded. Stochastic physical factors probably are more important than coactive patterns in shaping the zoobenthos communities of most lotic segments in the Colorado Basin.

Except for certain headwaters, nearly all reaches are influenced by stream regulation. The tailwaters below deep-release dams are characterised by a zoobenthos similar to that of cold springbrooks. Only chironomids and baetid mayflies, among insects, normally comprise a significant portion of the benthos. Non-insects such as amphipods, planarians, oligochaetes and snails (some of which did not occur prior to regulation) may also become abundant. Large segments of the Colorado and its major tributaries have become series of reservoirs and tailwaters, obscuring forever whatever vestige may remain of the indigenous lotic zoobenthos of the Colorado River system.

Acknowledgements

The authors express appreciation to Drs G. A. Cole, R. W. Pennak and J. A. Stanford for comments. Mr T. C. McCall, Arizona Game & Fish Dept, kindly provided unpublished data on zoobenthos below Glen Canyon Dam. Miss Nancy Flaming and Mrs Nancy Heisler typed the manuscript. Support was provided, in part, by a research grant from the Colorado Experiment Station to J. V. Ward.

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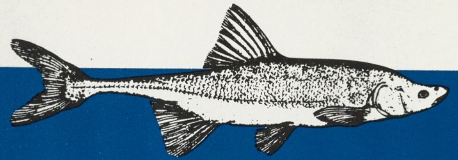


Bonytail Chub

The bonytail chub *(Gila elegans)* is the rarest of the endangered Colorado River fishes—and is close to extinction in the wild.

With its large fins and streamlined body, which tapers to pencil-like thinness in front of the tail, the bonytail appears to be midway between its close relatives, the roundtail chub and the humpback chub, in its adaptations to the river's torrential flows.

The bonytail, which reaches a maximum length of about 18 inches, was once found throughout the river system in main channels and the lower reaches of the larger tributaries. Today, however, no reproducing populations are known, and only a few individuals have been reported in the last 20 years.

The bonytail chub is protected as an "endangered species" under federal law and listed as "endangered" in Colorado and "protected" in Utah under state laws.

Humpback Chub

Perhaps because it favors deepwater canyon areas that are relatively hard to reach, the humpback chub *(Gila cypha)* was not known to science until 1946.

This remarkable fish, usually 12-16 inches long, has a number of distinctive features: prominent, smoothly rounded hump behind its head; small eyes; and long snout that overhangs its lower jaw. It's believed that these features help the fish swim through turbulent canyon waters.

Today the largest known populations of humpback chub exist in the Little Colorado River in the Grand Canyon and at Black Rocks and Westwater canyons on the upper mainstem of the Colorado. They are also found in smaller numbers in the Yampa River in Dinosaur National Monument, Desolation and Gray canyons on Utah's Green River and Cataract Canyon on the Colorado River.

The humpback is listed as "endangered" by the federal government and listed as "endangered" in Colorado and "protected" in Utah under state laws.

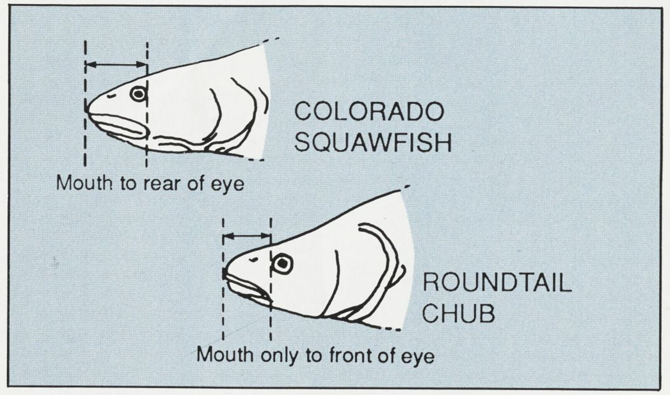
Colorado Squawfish

For millions of years, the Colorado squawfish *(Ptychocheilus lucius)* reigned as the top predator of the Colorado River. With its olive-green and gold back and silvery belly, it is an impressive animal—an efficient, torpedo-shaped hunter that historically reached weights of 50-80 pounds, lengths of 6 feet and, some scientists think, ages of 70 years and up.

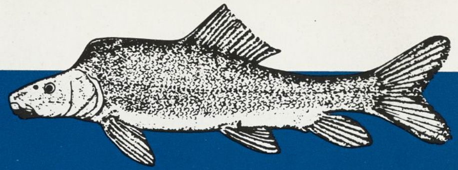
Early settlers called the fish "white salmon" or "Colorado salmon" or just "salmon," probably because of its large size and its habit of making long spawning runs. Old-timers also called the fish "good eating": A menu from an 1889 Christmas feast at Lee's Ferry lists "Colorado River Salmon" along with "Roast Turkey," "Arizona Apples" and "Plumb Pudding."

Once Colorado squawfish were so abundant throughout the river system that they were harvested by commercial fishermen. Today, wild populations are limited to the Upper Colorado Basin, especially in the Green, White and Yampa rivers, where the fish is occasionally taken by fishermen.

Anglers may confuse young squawfish with roundtail chub, which are still common in much of the Upper Colorado. The two can be told apart most easily using eye position: In the roundtail, the mouth extends just to the front of the eye; the Colorado squawfish's snout is longer, and thick folded lips extend to the rear of the eye. The fish readily hit artificial lures.



The Colorado squawfish is listed as "endangered" under the federal Endangered Species Act and has been designated "endangered" in Colorado and "protected" in Utah under state laws.



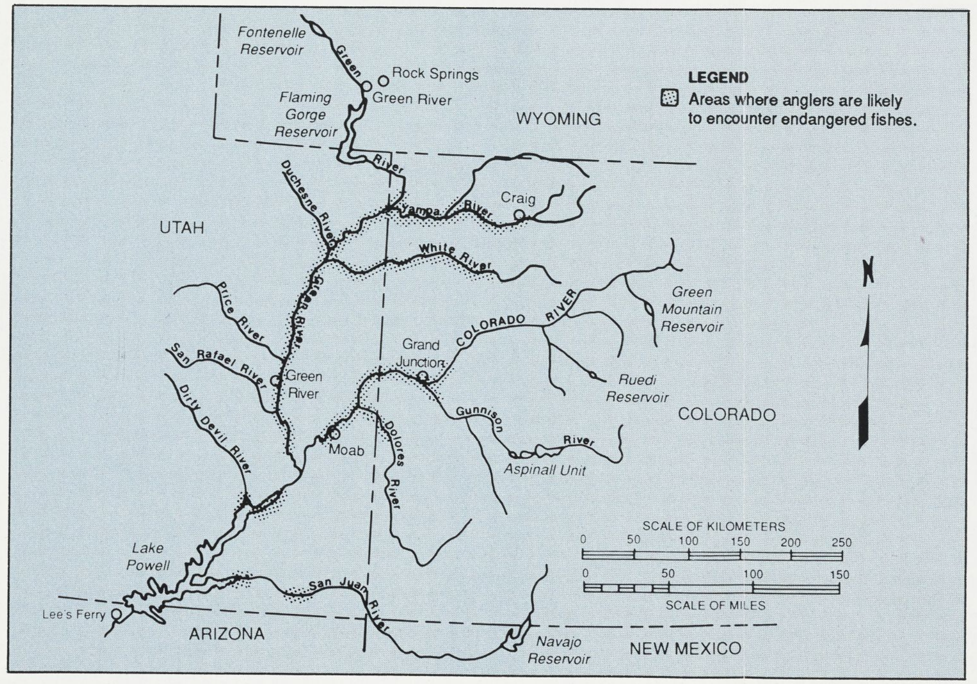
Razorback Sucker

The razorback sucker *(Xyrauchen texanus)*, one of the largest suckers in North America, may weigh as much as 12 pounds. The abrupt, bony, keel-edged hump that rises on its back just behind its head distinguishes this fish from all other suckers.

Perhaps the largest population of razorback suckers lives in Lake Mojave. However, this population appears to consist entirely of fish as much as 30-40 years old; though they do spawn, their young do not appear to survive to adulthood.

In unimpounded waters, the razorback is limited to Upper Basin rivers, especially the Green, Yampa and mainstem of the Colorado. The largest population, estimated at about 1,000 adults, lives in the Green River near Jensen, Utah. However, there is no documented proof of successfully reproducing fish in the Upper Basin. It is feared that as existing adults die off, the population will disappear.

Now listed as "protected" in Utah and "endangered" in Colorado under state laws, the razorback sucker has been proposed for federal protection as an "endangered species."



ENDANGERED FISH: Put Them Back Alive

Anglers can help prevent the loss of these unique natives of the Colorado River. The map below shows the areas where populations of one or more of these endangered fish are known. Please take special care when fishing in these areas.

Remember: It's more than good sportsmanship to return one of these fish to the water when it's accidentally hooked: Fines of up to $20,000 and even jail sentences are possible for willfully destroying one.

Fishermen have the responsibility of being able to identify the fish they catch. If you're unsure, please play it safe and follow these steps immediately to return the fish alive to the water:

1) If possible, leave the fish in the water while removing your hook.

2) Remove the hook gently; don't squeeze the fish or put your fingers in its gills.

3) If your hook is deeply embedded, cut the line instead of pulling out the hook.

4) Release the fish in quiet water—only after you're sure its equilibrium is restored. If it is necessary to help restore the fish's equilibrium, gently hold the fish facing upstream and move it slowly back and forth in the water.

If the fish is tagged, please record the tag's number and color, as well as time and place of the encounter, and report it to the Colorado Division of Wildlife, NW Region, 711 Independent Ave., Grand Junction, CO 81501 (303/248-7175), or the Utah Division of Wildlife Resources, Non-game Section, 1596 W. North Temple, Salt Lake City, UT 84116 (801/533-9333). This information will increase our understanding of these rare fishes, and you will have helped keep a vital part of the heritage of the Colorado River alive.

W.T. Lowe snapped this picture of his sons Jack (right) and Bill with Colorado squawfish caught at the mouth of Dominguez Creek, near Delta, Colorado, in 1942. (Photo courtesy of Jack Lowe)

Several of these unique species have not adapted well to the Colorado River of the 20th Century. Three species, the Colorado squawfish, the bonytail chub and the humpback chub, are endangered, and a fourth, the razorback sucker, is very rare. Reasons given for their decline include alteration and reduction of habitat and competition from non-native fish species.

Efforts are now underway throughout the Colorado system to save these residents of the river from extinction. A special recovery effort has targeted the Upper Basin—the part of the system above Lee's Ferry, Arizona. The challenge of the last years of this century is to balance development of the Upper Basin with the needs of its native species. To find ways for these creatures—veterans of one of nature's roughest rivers—to survive into the 21st Century.

This brochure is part of the information and education portion of the Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River Basin. That program represents a milestone in cooperation among federal and state agencies in Colorado, Utah and Wyoming, as well as water development and environmental interests. Its goal is to balance the protection and recovery of the Colorado River's endangered fish with continued water development in the Upper Basin.

The program includes coordinated state, federal and private efforts to improve habitat, provide streamflows at times and locations critical to the life cycles of the fish, reduce conflicts with non-native fish species and stock endangered fish to augment wild populations. For more information on the program, contact your local wildlife management agency or the U.S. Fish and Wildlife Service, Fish and Wildlife Enhancement, Denver, CO 80225.

Program Participants
- U.S. Fish & Wildlife Service
- U.S. Bureau of Reclamation
- Western Area Power Administration
- State of Colorado, Department of Natural Resources
- State of Utah, Department of Natural Resources
- State of Wyoming, State Engineer's Office

Colorado Wildlife Federation
National Audubon Society
Environmental Defense Fund

Colorado Water Congress
Utah Water Users Association
Wyoming Water Development Association

Brochure Design and Production: Western Area Power Administration
CDI Corporation-Midwest, Div. of CDI Corp.
Cover Artwork: CDI Corporation-Midwest-Connie Edwards

☆ U.S. GOVERNMENT PRINTING OFFICE: 1989 - 675-291

Swimming Upstream:

The Endangered Fish of the Colorado River

TIME AND THE COLORADO RIVER

The Colorado and its tributaries make up one of the world's most colorful river systems. From headwaters in the high mountains of Wyoming and Colorado, it drops more than two miles in elevation on a 1,700-mile journey to the Gulf of California. For long stretches of that distance, the river system is bounded by canyon walls.

The river has also earned its name: *Colorado*—"red" river. Before major dams tamed its flows, the river delivered more than 100,000 acre feet of sediment to the Gulf of California each year.

The harsh and spectacular country the river travels through also makes for a harsh and spectacular environment within the river itself. Flows fluctuate widely from season to season—and from year to year. Historic flows at Yuma, Arizona, have ranged from a few thousand cubic feet per second to almost 400,000 cubic feet per second.

It took tough and adaptable creatures to survive in this environment, which was isolated for thousands of years by high mountains. This vast period of isolation produced a variety of native fish species found nowhere else in the world.

The area where the Green and Yampa rivers come together, in Dinosaur National Monument, near the Colorado-Utah border. (Photo courtesy of the National Park Service, Dinosaur National Monument)

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