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the late appearance of *D. melanogaster* in the traps in the spring as compared to other *Drosophila* species all suggest that this species does not overwinter out-of-doors in Minnesota.

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ZOOLOGY

The Fish Fauna of the Mississippi River above St. Anthony Falls as Related to the Effectiveness of this Falls as a Migration Barrier

SAMUEL EDDY¹, JOHN B. MOYLE² and JAMES C. UNDERHILL¹

INTRODUCTION: At St. Anthony Falls, in Minneapolis, the Mississippi River drops 70 feet from the pool above to the pool below. This waterfall has been in existence and has probably been an effective barrier to upstream migration of fish for about 10,000 years. It originated at an erosion escarpment of glacial River Warren, near present Fort Snelling, following the withdrawal of the last (Mankato) continental ice sheet. Since then, this falls has retreated about eight miles to its present site by wearing away and undercutting the Ordovician strata over which the Mississippi flows (Sardeson, 1916). It is likely that the total height of this falls has always been about the same, although the sheer drop has at times been broken by cataracts.

The effectiveness of St. Anthony Falls as a fish migration barrier is borne out by a comparison of the fish faunas above and below. There are 123 species of fish known from Minnesota and contiguous Wisconsin waters below the falls but only 64 known from the extensive drainage area above. Many species that are common and characteristic below the falls are lacking above it. Obviously, the indigenous species now above the falls must either be: (1) fishes that have somehow circumvented the barrier of the falls or (2) fishes native to part of the upper basin before the last glaciation that survived in areas that were not covered by the two lobes of the last ice sheet. In addition to burial and alteration of pre-existing topography, aquatic habitat conditions must also be considered as possible barriers to migration; especially past and present water temperatures. Melt water from the glacial ice would be suited to cold-water but not to warm-water species. Under the present climate, however, many species of fish not found in the upper Mississippi drainage above the falls occur farther north in

the St. Croix drainage and in the Red River arctic drainage. The former at present connects with the Mississippi below St. Anthony Falls and the latter was once also connected with the lower Mississippi through glacial River Warren and glacial Lake Agassiz.

It appears, therefore, that the predominant features of fish distribution above St. Anthony Falls are ancient and can best be related to the immediate post-Pleistocene history of Minnesota, and also that St. Anthony Falls was an important factor in limiting the northward distribution of many species in the Mississippi drainage.

A likely connecting water by which St. Anthony Falls may have been bypassed in immediate post-Pleistocene time was glacial Lake Grantsburg. This lake formed behind a finger-like and eastward projecting sublobe of the Mankato ice and impounded water from the precursor of the present upper Mississippi River. For a time there was drainage around the edge of this Grantsburg sublobe into the St. Croix River and it is likely that free passage of fish was possible between the two drainages (Underhill 1957). It is possible also that this glacial lake and the waters feeding it contained fishes, especially cold-water fishes, that had survived in adjacent areas from the preceding inter-glacial period. Pollen and macrofossils from a site near the margin of the Grantsburg sublobe indicate that the climate was only slightly colder and probably drier than at present in the upper Mississippi drainage in late Mankato time (Fries, Wright, and Rubin, 1961).

For the past 50 years pollution of the Mississippi River at Minneapolis and St. Paul has caused low oxygen in the water as far downstream as Hastings, thus imposing a chemical barrier to upstream fish migration. This chemical barrier, however, seems to have been of little consequence in the general fish distribution pattern.

DISCUSSION OF FISH DISTRIBUTION: Only two species

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of ganoid fishes occur above the St. Anthony Falls; the bowfin (*Amia calva*) and the shortnose gar (*Lepisosteus platostomus*). The bowfin is a fairly common fish in weedy waters and is known from the Mississippi as far north as Lake Winnibigoshish, and was taken here by a stream survey crew in the summer of 1961. The shortnose gar, however, is known for only a short distance above St. Anthony Falls (Friedrich, 1933) and is evidently uncommon since it has not been taken in recent years.

In addition to the two ganoids already mentioned, two sturgeons (Acipenseridae) occur below the falls but not above. They are the lake sturgeon (*Acipenser fulvescens*) and the shovelnose sturgeon (*Scaphirhynchus platorhynchus*). Both in pre-pollution days, were present to the base of the falls. The lake sturgeon occurs in both the adjacent Red River and St. Croix River drainages and is especially abundant in some shallow lakes of the latter drainage, especially Pokegama and Cross lakes in Pine County. The paddlefish (*Polydon spathula*), was present to the base of the falls until 50 years ago, but is not known from the drainage above. The longnose gar (*Lepisosteus osseus*) occurs only in the more southern Minnesota waters of the Mississippi.

Neither the mooneye (*Hiodon tergisus*) nor the gold-eye (*H. alosoides*) is known from above the falls although both these Hiodontids occur below the falls and range northward in the Red River drainage where the goldeye is netted commercially in lakes. The herring family (Clupeidae) is represented below the falls by the gizzard shad (*Dorosoma cepedianum*), here a very common fish, and by the skipjack (*Alosa chrysochlorus*); but neither species is known from above the falls.

Four species of trout (Salmonidae) are now found above the falls in the colder tributary streams and in a few cold-water lakes. Three of these, the brown trout (*Salmo trutta*), the rainbow trout (*Salmo gairdneri*) and the brook trout (*Salvelinus fontinalis*) are certainly not native and have been introduced by fish culturists since 1870. The lake trout (*Salvelinus namaycush*) is native to the adjacent arctic drainage and, although early reported from Lake Pokegama in Itasca County by Cox (1897), may also have been introduced.

The distribution pattern of the brook trout poses a special problem. It was native to cold-water tributaries below the falls, to tributaries of the St. Croix and to Lake Superior but evidently was not present at early and high stages of Lake Superior since it did not occur in streams above the high falls along the North Shore (Smith and Moyle, 1944).

Whitefishes of the family Coregonidae are found in many of the cooler lakes of the Mississippi drainage above the falls as well as in the adjacent arctic drainage. Both the tullibee (*Coregonus artedi*) and the whitefish (*C. clupeaformis*) are cold-water fishes that are usually confined to lakes. They may well have been inhabitants of glacial Lake Grantsburg and survivors in the upper Mississippi drainage from pre-Mankato time. Tullibee have been taken from several lakes tributary to the Mississippi south of St. Anthony Falls.

The sucker family (Catostomidae) is represented in the Mississippi drainage below St. Anthony Falls by at least 16 species. Most or all of these probably reached the base of the falls in pre-pollution days. Only four species of this family are known from above the falls. They are the white sucker (*Catostomus commersoni*) which is abundant throughout; the northern redhorse (*Moxostoma macrolepidotum*), a common fish of large streams; the silver redhorse (*M. anisurum*) which is locally abundant in such places as the mouth of the Crow River; and the bigmouth buffalo (*Ictiobus cyprinella*) which is uncommon in the upper drainage.

In Minnesota and adjacent waters of the Mississippi drainage below the falls there are 42 species of the minnow family (Cyprinidae). Of these at least 12 are southern species which possibly have never ranged as far north as the falls. Twenty-three native minnows and the introduced carp have been collected above the falls. The fine-scaled dace, (*Chrosomus neogaeus*), a northern species which is characteristic of the Arctic and Lake Superior drainages, was collected in 1960 at the source of the Mississippi River below Lake Itasca (Nordlie, *et al.*, 1961). Its appearance at the Mississippi headwaters suggests that it is a recent migrant from the Arctic drainage. There is also the possibility that it has been introduced as a bait minnow. Although reported by Green (1935) from Mississippi tributaries in Wisconsin below the falls, this fish has not been taken in similarly located Minnesota tributaries.

The carp (*Cyprinus carpio*), has only recently gained access to the river above the falls. Surber (1920) reported that carp were unknown above St. Anthony Falls prior to 1920. It was probably accidentally carried around the falls and by 1929 was abundant immediately above them. By 1962 its range has extended northward in the Mississippi River to the dam at Little Falls and still farther northward in the Rum River drainage to Big Pine Lake in Aitkin County. Carp have, however, also become established in some headwater lakes of the Crow Wing River near Alexandria, probably from an early planting made in the 1880's and which was long landlocked. They are now abundant in Mary and Lobster lakes. An attempt is being made to limit their downstream spread in the Mississippi drainage by use of fish barriers.

Of the 24 species of the minnow family now known from above the falls, the 18 that are starred (*) occur in the headwaters at Lake Itasca and those marked with a dagger (†) were taken between the Pokegama and Winnibigoshish dams in Itasca County by a stream survey crew during the summer of 1961.

Cyprinus carpio Linnaeus, carp, introduced
Semotilus atromaculatus (Mitchill), creek chub*
S. margarita nachtriebi (Cox), northern pearl dace*
Rhinichthys atratulus meleagris Agassiz, western blacknose dace*
R. cataractae (Valenciennes), longnose dace*
Hybopsis biguttata (Kirkland), hornyhead chub*
Chrosomus neogaeus (Cope), finescale dace*
C. eos Cope, northern redbelly dace*
Notemigonus crysoleucas (Mitchill), golden shiner*†

Notropis atherinoides Rafinesque, emerald shiner*
N. cornutus frontinalis (Agassiz), northern common shiner*†
N. blennioides (Girard), river shiner
N. hudsonius (Clinton), spottail shiner*†
N. heterodon (Cope), blackchin shiner*
N. spilopterus (Cope), spotfin shiner
N. dorsalis (Agassiz), bigmouth shiner*†
N. stramineus (Cope), sand shiner*
N. volucellus (Cope), mimic shiner*†
N. heterolepsis Eigenmann and Eigenmann, blacknose shiner*†
N. anogenus (Forbes), pugnose shiner
Hybognathus hankinsoni Hubbs, brassy minnow
Pimephales promelas Rafinesque, fathead minnow*†
P. notatus (Rafinesque), bluntnose minnow*†
Campostoma anomalum (Rafinesque), stoneroller

The catfish family (Ictaluridae) is represented by seven species below the falls but by only four species above. The bullheads, *Ictalurus melas*, *I. natalis* and *I. nebulosus* are widespread above the falls, as is the madtom, (*Schilbeodes gyrinus*). The channel catfish, (*Ictalurus punctatus*) and the flathead catfish (*Pylodictis olivaris*) both of which are characteristic of the larger rivers below the falls are unknown from above it. Similarly, the stonecat (*Noturus flavus*) is found in many of the tributaries of the lower Mississippi River but is unknown from the upper river. The latter species is known northward from small tributaries of the St. Croix River. The channel catfish occurs both in the St. Croix River and the St. Louis River and is found as far north as lakes on the Mesabi Range (Moyle, 1953).

The mud minnow, *Umbra limi*, is widely distributed above and below the falls. The pike family (Esocidae) is represented by the northern pike (*Esox lucius*) and the muskellunge (*Esox masquinongy*) both above and below the falls. The killifish, (*Fundulus diaphanus*) and the troutperch (*Percopsis omiscomaycus*) are also common both above and below the falls.

The only representative of the family Aphredoderidae, the pirateperch (*Aphredoderus sayanus*) occurs in the sluggish waters of the Mississippi River as far north as Winona, Minnesota, but in all probability it never reached the base of the falls. The burbot (*Lota lota*) is widespread in the upper Mississippi River drainage in the larger deeper lakes. It also occurs in the Lake Pepin region below the falls.

The perch family (Percidae) is represented in the drainage below the falls by the walleye (*Stizostedion vitreum*), the sauger (*S. canadense*), the perch (*Perca flavescens*), and by 15 species of darters. Only six species of the family occur above the falls. The walleye, although introduced into many lakes, is native to many of the larger streams and lakes above the falls. The perch is common throughout the state. The sauger has not appeared in any collections from above the falls during the past 50 years nor has it been seen by lake survey crews in recent years. Cox (1897) reported it from Big Gull Lake before 1895, unfortunately he failed to state

whether this was the Gull Lake of the Upper Mississippi River drainage. It occurs north of St. Anthony Falls in the Red River and connected border lakes and in the St. Croix River.

Fifteen species of darters are found in the lower Mississippi River drainage in Minnesota. Two of the species are not known north of Red Wing, Minnesota and it is doubtful that they ever reached the base of the falls. Only four of our most widespread darters are present above the falls. The Johnny darter (*Etheostoma nigrum*) is generally present in lakes and streams above the falls. The Iowa darter (*E. exilis*) is common above and below the falls but occurs in larger numbers above the falls. The least darter (*E. microperca*) has been taken only occasionally. The log perch (*Percina caprodes*), is common in all the larger streams of the upper Mississippi River drainage.

Seven species of the sunfish family (Centrarchidae) are widely distributed throughout the Mississippi River drainage above the falls. These are the largemouth bass (*Micropterus salmoides*), and smallmouth bass (*M. dolomieu*), the black crappie (*Pomoxis nigromaculatus*), the bluegill (*L. macrochirus*), the pumpkinseed (*L. gibbosus*), the green sunfish (*L. cyanellus*) and the rock bass (*Ambloplites rupestris*). The white crappie (*Pomoxis annularis*) and the orangespot sunfish (*Lepomis humilis*) have never been taken above the falls but are common in the river south of the falls and in the Minnesota River west to Bigstone Lake. Another centrarchid, the warmouth (*Chaenobryttus gulosus*) is not known to occur as far north as St. Anthony Falls.

None of the sea basses of the family Serranidae occur above the falls. The white bass (*Roccus chrysops*) probably reached the base of the falls in pre-pollution time but the yellow bass (*Morone interrupta*) does not range this far north.

The sheepshead (*Aplodinotus grunniens*) is also unknown from the upper Mississippi River. This species is common in the lower Mississippi River and ranges far northward in the Red River drainage.

The brook silversides (*Labidesthes sicculus*), our sole representative of the silverside family (Atherinidae) is widespread both above and below the falls. Two species of the family Cottidae, the northern sculpin (*Cottus bairdi*) and the slimy sculpin (*C. cognatus*) are present both above and below the falls especially in smaller streams. The latter species is known only from a single specimen from Kabekona River.

The stickleback family (Gasterosteidae) is commonly represented in the headwater streams by the brook stickleback (*Eucalia inconstans*) both above and below the falls. The ninespine stickleback (*Pungitius pungitius*) is probably a recent invader in the headwaters region of the upper Mississippi River (Nordlie et al. 1961).

Slightly over half of 123 species of fish known to be present in the lower Mississippi River basin in Minnesota have reached the river above the falls. Since many of those species not found north of the falls are common in the St. Croix, Minnesota and Red rivers there can be little doubt about the effectiveness of St. Anthony Falls

as a barrier to upstream movement of fishes. The lock and dam system now under construction to open the upper river to barge traffic will probably allow certain species not now present to invade the upper Mississippi River. This will provide an excellent opportunity to determine the use of locks by fishes and also may provide information on the rates of movement of certain species. Opening of these locks may provide an almost unique opportunity to determine the role of a physical barrier in determining the limits of distribution of fish species. It would appear that several species presently restricted to the lower river will, if they pass the lock, find habitats and ecological conditions in the upper river very similar if not identical to those they occupied downstream. Invasion of the upper river by such species may also bring about changes in the relative abundance of the species now present, changes which may be of importance from a practical as well as an academic point of view and which may give some insight into the role of competition between the species concerned.

Extension of ranges of fishes in the upper river is probably still taking place. Forty-one or approximately 65% of the species in the upper Mississippi River are known from the headwaters region at Lake Itasca. The absence of certain species from the headwaters might reasonably be explained by the greater diversity of habitats in the basin south of Bemidji, Minnesota, as well as by occurrence of dams. Many of the species that have not reached the headwaters region are species which have rather wide habitat tolerances and are common in both streams and lakes. These could be expected to thrive at the headwaters. Establishment of a particular species by means other than recent immigration into the watershed or slow migration upstream over a long period of time — especially by accidental introduction — can never be disproved. Similarly it is possible that rarity of some species has made their capture unlikely. The fact that for over thirty years classes at the Lake Itasca Forestry and Biological Station have been sampling annually for fishes in the lakes and streams in the region weakens the argument for inadequate sampling. An example of probable expanding range is the stoneroller. It is known from the Mississippi River only south of St. Cloud, but is common in the Rum River and its tributaries. Importance of continued sampling of our fish populations cannot be ignored.

It seems likely that single fish or a few fish or a particular species not established in the upper watershed occasionally have found and still find means of entering it; live out their life span; and then disappear. For example there is a single authentic sight record for the American eel (*Anguilla rostrata*) taken by a survey crew in 1960 at the outlet of Little Rock Lake, near Sartell, which is well above St. Anthony Falls. Eel still occurs and were once quite common below the falls. Similarly a 37-pound catfish was taken from the Mississippi River near Fort Ripley, above the falls in 1959 and identified by Fisheries Biologist J. M. Maloney of Brainerd as a blue catfish (*Ictalurus furcatus*). Also in 1949 a brook lamprey was taken from Pelican Lake in Crow

Wing County; the only known occurrence of a lamprey of any kind in the upper drainage basin. There is also a report of a sturgeon illegally speared in Crooked Lake (T. 45, R. 28) in Crow Wing County. Unfortunately these reports cannot be authenticated as specimens of these fishes were not preserved as records.

TABLE 1. Fishes of the Mississippi River Basin found above and below St. Anthony Falls (Occurrences starred (*) are introduced species; with dagger (†), reported by Green, 1935).

	Below Falls	Above Falls
Petromyzonidae		
<i>Ichthyomyzon unicuspis</i>	+	—
<i>I. castaneus</i>	+	—
<i>Entosphenus (Lampetra) lamotteni</i>	+	+
Polyodontidae		
<i>Polyodon spathula</i>	+	—
Acipenseridae		
<i>Acipenser fulvescens</i>	+	—
<i>Scaphyrhynchus platyrhynchus</i>	+	—
Lepisosteidae		
<i>Lepisosteus platostomus</i>	+	+
<i>L. osseus</i>	+	—
Amiidae		
<i>Amia calva</i>	+	+
Coregonidae		
<i>Coregonus clupeaformis</i>	—	+
<i>C. artedi</i>	+	+
Salmonidae		
<i>Salmo fario</i>	+*	+*
<i>S. gairdneri</i>	+*	+*
<i>Salvelinus fontinalis</i>	+	+*
<i>S. namaycush</i>	—	+
Hiodontidae		
<i>Hiodon tergisus</i>	+	—
<i>H. alosoides</i>	+	—
Clupeidae		
<i>Dorosoma cepedianum</i>	+	—
<i>Alosa chrysochloris</i>	+	—
Castostomidae		
<i>Cycleptus elongatus</i>	+	—
<i>Ictiobus cyprinella</i>	+	+
<i>I. niger</i>	+	—
<i>I. bubalus</i>	+	—
<i>Carpionodes cyprinus</i>	+	—
<i>C. carpio</i>	+	—
<i>C. velifer</i>	+	—
<i>Mosostoma duquesnei</i>	+	—
<i>M. erythrurum</i>	+	—
<i>M. anisurum</i>	+	+
<i>M. macrolepidotum</i>	+	+
<i>Hypentelium nigricans</i>	+	—
<i>Catostomus commersoni</i>	+	+
<i>Erimyzon succetta</i>	+	—
<i>Minytrema melanops</i>	+	—
Cyprinidae		
<i>Cyprinus carpio</i>	+*	+*
<i>Notemigonus crysoleucas</i>	+	+
<i>Semotilus atromaculatus</i>	+	+
<i>S. margarita</i>	+	+
<i>Gila elongata</i>	+	—
<i>Opsopoeodus emilae</i>	+	—
<i>Chrosomus erythrogaster</i>	+	—
<i>C. eos</i>	+	+
<i>Chrosomus neogaeus</i>	+†	+
<i>Hybopsis biguttata</i>	+	+
<i>H. storeriana</i>	+	—

TABLE 1.—(Continued)

	Below Falls	Above Falls
<i>H. aestivalis</i>	+	—
<i>H. X-punctata</i>	+	—
<i>Rhinichthys atratulus</i>	+	+
<i>R. cataractae</i>	+	+
<i>Phenacobius mirabilis</i>	+	—
<i>Notropis atherinoides</i>	+	+
<i>N. rubellus</i>	+	—
<i>N. cornutus</i>	+	+
<i>N. roseus</i>	+	—
<i>N. heterodon</i>	+	+
<i>N. hudsonius</i>	+	+
<i>N. blennioides</i>	+	+
<i>N. dorsalis</i>	+	+
<i>N. amnis</i>	+	—
<i>N. spilopterus</i>	+	+
<i>N. stramineus</i>	+	+
<i>N. heterolepis</i>	+	+
<i>N. volucellus</i>	+	+
<i>N. agnogenus</i>	+	+
<i>Dionda nubila</i>	+	—
<i>Hybognathus hankinsoni</i>	+	+
<i>H. nuchalis</i>	+	—
<i>Pimephales perspicuus</i>	+	—
<i>P. notatus</i>	+	+
<i>P. promelas</i>	+	+
<i>Campostoma anomalum</i>	+	+
Ictaluridae		
<i>Ictalurus punctatus</i>	+	—
<i>I. nebulosus</i>	+	+
<i>I. melas</i>	+	+
<i>I. natalis</i>	+	+
<i>Pylodictus olivaris</i>	+	—
<i>Schilbeodes gyrinus</i>	+	+
<i>Noturus flavus</i>	+	—
Umbridae		
<i>Umbra limi</i>	+	+
Esocidae		
<i>Esox lucius</i>	+	+
<i>E. masquinongy</i>	+	+
Anguillidae		
<i>Anguilla rostrata</i>	+	+
Cyprinodontidae		
<i>Fundulus diaphanus</i>	+	+
Gadidae		
<i>Lota lota</i>	+	+
Percopsidae		
<i>Percopsis omiscomaycus</i>	+	+
Aphredoderidae		
<i>Aphredoderus sayanus</i>	+	—
Antherinidae		
<i>Labidesthes sicculus</i>	+	+
Serranidae		
<i>Roccus chrysops</i>	+	—
<i>Morone interrupta</i>	+	—
Centrarchidae		
<i>Micropterus salmoides</i>	+	+
<i>M. dolomieu</i>	+	+
<i>Chaenobryttus coronarius</i>	+	—
<i>Lepomis cyanellus</i>	+	+
<i>L. gibbosus</i>	+	+
<i>L. macrochirus</i>	+	+
<i>L. humilis</i>	+	—
<i>Ambloplites rupestris</i>	+	+
<i>Pomoxis annularis</i>	+	+
<i>P. nigromaculatus</i>	+	+
Percidae		
<i>Stizostedion canadense</i>	+	—
<i>S. vitreum</i>	+	+

TABLE 1.—(Continued)

	Below Falls	Above Falls
<i>Perca flavescens</i>	+	+
<i>Percina maculata</i>	+	—
<i>P. evides</i>	+	—
<i>P. phoxocephala</i>	+	—
<i>P. shumardi</i>	+	—
<i>P. carprodes</i>	+	+
<i>Ammocrypta asprella</i>	+	—
<i>A. clara</i>	+	—
<i>Estheostoma nigrum</i>	+	+
<i>E. chlorosomum</i>	+	—
<i>E. zonale</i>	+	—
<i>E. asprigene</i>	+	—
<i>E. exile</i>	+	+
<i>E. caeruleum</i>	+	—
<i>E. flabellare</i>	+	—
<i>E. microperca</i>	+	+
Scianidae		
<i>Aplodinotus grunniens</i>	+	—
Cottidae		
<i>Cottus cognatus</i>	+	+
<i>C. bairdi</i>	+	+
Gasterosteidae		
<i>Eucalia inconstans</i>	+	+
<i>Pungitius pungitius</i>	—	+

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