IN SEARCH OF MINNESOTA'S CROSSOVER CONNECTIONS

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I have always been fascinated with fish distribution. How did they get to where they are today? Of course since humans have arrived on the scene, we have played a major role in spreading species around both intentionally through stocking or accidentlly via navigation and drainage projects. However, a pet peeve of mine is the rush to judgment of so many biologists to conveniently dismiss new occurrences in drainages or disjunct localities as bait-bucket releases. One case in point was the 1974 discovery of Northern Sunfish (*Lepomis peltastes*) in Minnesota from a very isolated lake miles inside the Boundary Waters Canoe Area Wilderness. Access to the lake is restricted to non-motorized watercraft requiring several long and rugged portages. The initial assumption regarding the origin of this population was an illegal introduction; however, the possibility of being a natural occurrence was not ruled out (Phillips et al. 1982). Since then additional specimens have been found mislabeled in museum collections and additional fish surveys revealed the original occurrence is part of a spotty, but natural range through portions of several Great Lakes states and southern Ontario. Nevertheless, the position persists today in some circles that the Northern Sunfish is an introduced species in Minnesota.

Over three decades ago, I received the just released *Fishes of Wisconsin* (Becker 1983) and immediately dove into the most comprehensive work done to date in the upper Midwest. I eventually read it cover to cover, but one of the most fascinating topics covered was crossover connections where intermittent fish passage corridors can form between drainages during high water periods. Becker listed several possible crossovers, but highlighted the low divide between the Fox and Wisconsin rivers at Portage (Figure 1) where floodwaters were deep enough to float canoes and barges. A navigation canal was completed in 1837 and widened with locks in 1876. This crossover is the suspected source of Mississippi River species (i.e., Shortnose Gar *Lepisosteus platostomus*, Bullhead Minnow *Pimephales vigilax*, Pugnose Minnow *Opsopoeodus emiliae*, Blackstripe Topminnow *Fundulus notatus*, Warmouth *Lepomis gulosus*, Western Sand Darter *Ammocrypta clara*, and River Darter *Percina shumardi*) in the Lake Michigan basin. John Lyons (Wisconsin Department of Natural Resources and NANFA member) believes at least 15 additional species have crossed this natural flood connection over the last several thousand years rather than just the period following the construction of the navigation canal. He noted early historical accounts report spring flooding of the Wisconsin River flowing down the Fox River for several days at a time.

Crisscrossing Minnesota doing fish surveys for more than 40 years I have become more and more intrigued with road signs marking continental and drainage divides.

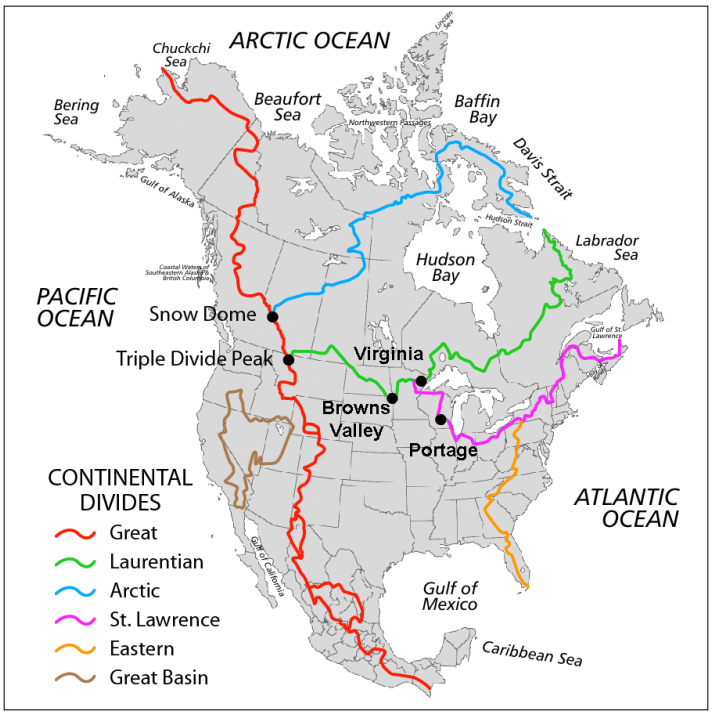

Figure 1. North American continental divides. http://www.halfwayanywhere.com/trails/continental-divide-trail/what-is-the-continental-divide-trail/

Photos and maps by the author unless otherwise indicated.

Figure 2. Laurentian divide and crest near Virginia, MN.

Figure 3. Laurentian divide near Browns Valley, MN.

A few are obvious such as portions of the Laurentian divide in northeastern Minnesota where today a range of hills, that were once lofty mountains a "billion" years ago separate the Great Lakes from the Hudson Bay drainages (Figure 2).

However, more often than not, the landscapes are large lakes or wetlands perched on the cusp of divides showing no perceptible rise or fall whatsoever. One example is the same Laurentian divide to the west on the South Dakota border near Browns Valley, Minnesota. Here, only a highway with a normally stagnant culvert separates the Gulf of Mexico via the Minnesota River from Hudson Bay via the Red River of the North, but water will flow either way dependent on which side is higher (Figure 3).

Six fishes reported north of the divide are assumed not native to the Red River of the North drainage, but do occur south of the divide in the Minnesota River and may have utilized this crossover connection (see Figure 6 number 27). The "alien" species include: Greater Redhorse (*Moxostoma valenciennesi*), Northern Hog Sucker (*Hypentelium nigricans*), Orangespotted Sunfish (*Lepomis humilis*), Smallmouth Buffalo (*Ictiobus bubalus*), White Bass (*Morone chrysops*), and White Crappie (*Pomoxis annularis*). All are indigenous to Minnesota, but this breach is an early warning sign of what is coming and eliminating this crossover could become the last ditch effort to stop Asian Carp invading the Hudson Bay basin. In December 2015 commercial fishermen caught the first Grass Carp (*Ctenopharyngodon idella*) from the Minnesota River near New Ulm. This was followed with the first Bighead Carp (*Hypophthalmichthys nobilis*) in February 2016 at the same location.

This low divide once was the spillway for Glacial Lake Agassiz that drained melt water of wasting glaciers following the last Ice Age and the source of the Glacial River Warren. The present day Minnesota River and Mississippi down-

Figure 4. St. Anthony Falls by George Catlin (1796–1872).

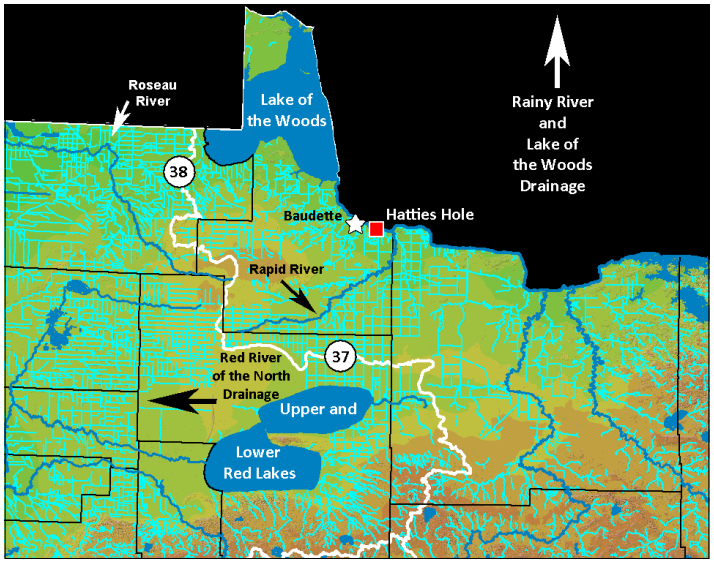

Figure 5. Freshwater Drum locality at Hatties Hole. Numbers 37 and 38 are possible crossovers between drainages.

stream of their confluence are mere trickles in comparison to Warren, which cut an enormous valley spanning up to five miles wide and 250 feet deep providing incredibly scenic vistas today (Wikipedia contributors).

There are at least two instances in Minnesota where crossovers were created from fairly recent human intervention. St. Anthony Falls in Minneapolis (Figure 4) is the best known. For 10,000 years since the last Ice Age, the falls functioned as a migration barrier with 123 fishes known below the falls, but only 63 above (Eddy et al. 1963). However, since the construction of the Upper and Lower St. Anthony navigation locks in 1963 at least eight species have breached the historic barrier and now occur in the lower Mississippi Headwaters drainage. These include: Blackside Darter (*P. maculata*), Bullhead Minnow, Channel Catfish (*Ictalurus punctatus*), Flathead Catfish (*Pylodictis olivaris*), Gizzard Shad (*Dorosoma cepedianum*), Northern Hog Sucker, Orangespotted Sunfish, and Stonecat (*Noturus flavus*) (Hatch et al. 2003). The barrier was restored in 2015 with the closure of the upper lock as a control measure to prevent the spread of Bighead and Silver Carp (*H. molitrix*), but the jury remains out if the closure was done in time.

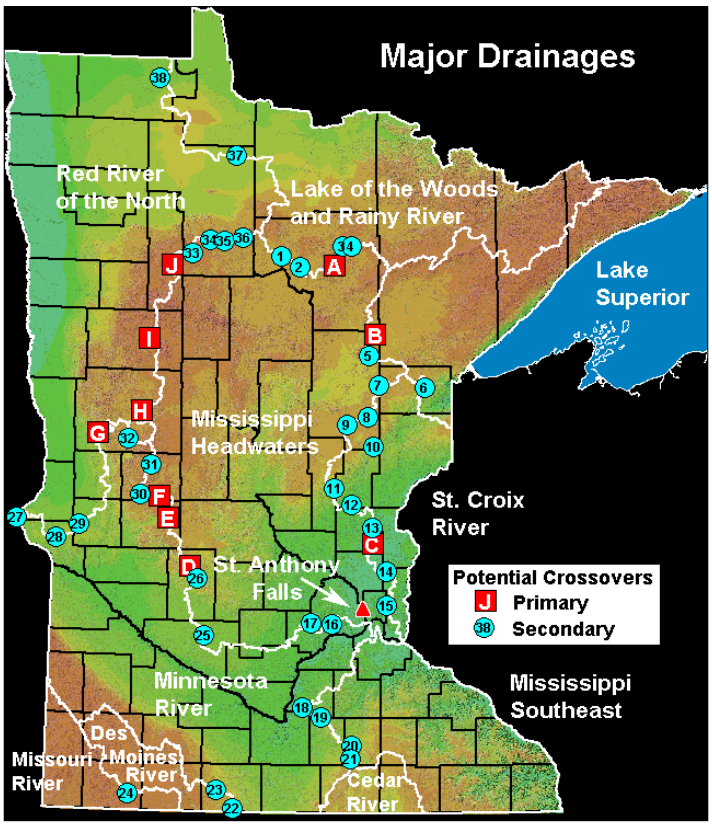

Figure 6. Minnesota's major drainages and potential crossovers (map key in Table 2).

The second case in point was discovered by accident when in 2001 an angler caught a Freshwater Drum (*Aplodinotus grunniens*) at Hatties Hole in the Rainy River on the Ontario–Minnesota border. The species had never been reported from the Lake of the Woods–Rainy River drainage, but does occur over a virtually non-existenet divide through a great expanse of flat-as-a-pancake peatlands in the Red Lakes, which is in the Red River of North drainage. Countless connections of human origin may occur in the general vicinity of crossover 37 (Figure 5). A century ago there was a massive effort to drain the peatlands for agriculture through a vast system of ditches that cross the drainage at numerous points. They have not been maintained in several decades, but most still flow today, providing multiple pathways to the Rainy River. There is possibly an alternate route from the Roseau River to the west also via ditches at crossover 38. The appearance of Freshwater Drum in the Rainy River is likely not a source of concern. However, it may serve as an early warning of "Barbarians at the Gate" since Common Carp (*Cyprinus carpio*) occur

Figure 7. Sensitive species: male and female Northern Sunfish (left) and male Least Darter (right).

in the Red Lakes south of crossover 37, but remain absent, for now, in Lake of the Woods drainage.

In 2013, I used a 500,000 plus record distribution database to produce range maps for all 164 fish species that occur in Minnesota. Displaying records spatially on a map is an amazing tool that often reveals overlooked occurrences missed in routine data queries. Potential crossovers surfaced between both continental, and also, watershed divides within major drainages. Typically, a crossover occurred in a watershed's headwaters where one or more species were common on one side and appeared to "bleed" over establishing a beachhead, which more often than not remains localized and does not spread. The map's shaded relief background usually revealed a pass (i.e., lakes, wetlands, or valleys) on the divide where suspected connections occurred. However, literature searches in other disciplines such as geology, glaciation, soils, and hydrology are mandatory to confirm crossovers existed since the last Ice Age. Furthermore, DNA studies need to be run on suspected populations to determine how similar or different they may be.

I identified 48 possible crossovers based on distribution (Figure 6) and 22 fish species (Table 1) which may have crossed divides into adjacent drainages and watersheds within drainages. The coordinates listed for crossovers should be viewed as general localities since multiple potential "passes" often occur in close proximity to each other (Table 2).

However, I must emphasize stocking and bait-pail introductions can never be entirely ruled out. I used a very arbitrary and subjective "personal hedge filter" to sort the crossovers into confidence levels of primary and secondary based on each species' relation to human activities. Primary crossovers involve extremely sensitive fishes which have no history of stocking or exhibit very high mortality under the crowded conditions in a bait pail. Secondary crossovers may very well be valid, however, most of these species have a history of introductions as game, forage, and/or bait species; transfers from long-defunct fish rescue programs, or agricultural and navigation projects (e.g., American Eel's, *Anguilla rostrata*, presence in Lake Superior via the Welland Canal that bypasses Niagara Falls).

The five sensitive species used to delineate primary crossovers were Mottled Sculpin (*Cottus bairdii*), Rainbow (*Etheostoma caeruleum*) and Least darters (*E. microperca*), Northern Sunfish, and Pugnose Shiner (Table 1, Figure 7). All are restricted to lakes and streams of exceptional water quality and habitat. The Mottled Sculpin is often a spe-

Figure 8. Crossover masters: Yellow Bullhead (left) and Banded Killifish (right).

Table 1. Species utilization of potential crossovers. Sensitive species are highlighted in yellow.

Species Code	Common Name	Scientific Name	Crossover Tally	Map Key (Figure 6)
A	Yellow Bullhead	*Ameiurus natalis*	24	A, J, 1–4, 6, 7, 11–15, 18–24, 30, 33, 35, 36
B	Bowfin	*Amia calva*	13	D–H, 2, 13–16, 18, 19, 31
C	Freshwater Drum	*Aplodinotus grunniens*	2	37, 38
D	Central Stoneroller	*Campostoma anomalum*	3	G, I, 25
E	Cisco	*Coregonus artedi*	12	F–H, 6–10, 31–33, 36
F	Mottled Sculpin	*Cottus bairdii*	4	C, H, J, 33
G	Rainbow Darter	*Etheostoma caeruleum*	1	G
H	Least Darter	*Etheostoma microperca*	6	B, D–H
I	Banded Killifish	*Fundulus diaphanus*	22	A, D–H, J, 2, 9, 10, 13, 15–18, 26, 30, 31, 33, 34, 37, 38
J	Northern Hog Sucker	*Hypentelium nigricans*	2	G, 27
K	Smallmouth Buffalo	*Ictiobus bubalus*	1	27
L	Brook Silverside	*Labidesthes sicculus*	5	12–14, 18, 26
M	Longnose Gar	*Lepisosteus osseus*	2	G, 19
N	Shortnose Gar	*Lepisosteus platostomus*	1	18
O	Orangespotted Sunfish	*Lepomis humilis*	7	18–21, 27–29
P	Northern Sunfish	*Lepomis peltastes*	2	A, I
Q	White Bass	*Morone chrysops*	3	16, 19, 27
R	Greater Redhorse	*Moxostoma valenciennesi*	1	27
S	Pugnose Shiner	*Notropis anogenus*	8	A, B, D–H, 17
T	Spottail Shiner	*Notropis hudsonius*	12	2, 5, 6, 11, 13, 14, 16–19, 30, 31
U	Weed Shiner	*Notropis texanus*	3	G–I
V	White Crappie	*Pomoxis annularis*	1	27

Table 2. Potential crossover connections in Minnesota based on species distribution. The map key applies to crossovers in Figure 6. Locations are approximate due to multiple possible crossovers visible in vicinity of coordinates on the shaded relief map layer. Primary crossovers have a higher level of confidence due to association with sensitive species and are highlighted in yellow.

Map Key	Species Code (Table 1)	Basins	Major Drainages (Figure 6)	General Locality	County	Latitude	Longitude
A	A, I, P, S	Gulf of Mexico–Hudson Bay	Mississippi Headwaters–Lake of the Woods	8.0 miles SE of Alder	Itasca	47.50345	-93.54571
B	H, S	Gulf of Mexico–Gulf of St. Lawrence	Mississippi Headwaters–Superior	3.6 miles south of Wawina	Aitkin	47.00076	-93.10914
C	F	Gulf of Mexico	Mississippi Headwaters–St. Croix	0.2 miles south of Weber	Isanti	45.47229	-93.12373
D	B, H, I, S	Gulf of Mexico	Mississippi Headwaters–Minnesota	3.7 miles west of New London	Kandiyohi	45.29253	-95.01808
E	B, H, I, S	Gulf of Mexico	Mississippi Headwaters–Minnesota	6.1 miles east of Glenwood	Pope	45.63569	-95.26568
F	B, E, H, I, S	Gulf of Mexico	Mississippi Headwaters–Minnesota	0.3 miles NW of Forada	Douglas	45.79408	-95.36104
G	B, D, E, G, H, I, J, M, S, U	Gulf of Mexico–Hudson Bay	Minnesota–Red River of the North	3.5 miles SE of Fergus Falls	Otter Tail	46.24721	-96.02503
H	B, E, F, H, I, S, U	Gulf of Mexico–Hudson Bay	Mississippi Headwaters–Red River of the North	1.0 miles SW of Ottertail	Otter Tail	46.41701	-95.57368
I	D, P, U	Gulf of Mexico–Hudson Bay	Mississippi Headwaters–Red River of the North	6.5 miles west of Ponsford	Becker	46.94492	-95.51611
J	A, F, I	Gulf of Mexico–Hudson Bay	Mississippi Headwaters–Red River of the North	3.2 miles SW of Shevlin	Clearwater	47.48934	-95.29140
1	A	Gulf of Mexico–Hudson Bay	Mississippi Headwaters–Lake of the Woods	4.2 miles south of Squaw Lake	Itasca	47.57233	-94.12326
2	A, B, I, T	Gulf of Mexico–Hudson Bay	Mississippi Headwaters– Lake of the Woods	5.1 miles SE of Inger	Itasca	47.49638	-93.91694
3	A	Gulf of Mexico–Hudson Bay	Mississippi Headwaters– Lake of the Woods	11.2 miles SE of Bigfork	Itasca	47.65141	-93.45669
4	A	Gulf of Mexico–Hudson Bay	Mississippi Headwaters– Lake of the Woods	14.8 miles SE of Bigfork	Itasca	47.64404	-93.37285
5	T	Gulf of Mexico–Gulf of St. Lawrence	Mississippi Headwaters–Superior	4.6 miles north of Balsam	Aitkin	46.84690	-93.17622

Map Key	Species Code (Table 1)	Basins	Major Drainages (Figure 6)	General Locality	County	Latitude	Longitude
6	A, E, T	Gulf of Mexico–Gulf of St. Lawrence	St. Croix–Superior	0.8 miles west of Atkinson	Carlton	46.61534	-92.58158
7	A, E	Gulf of Mexico	Mississippi Headwaters–St. Croix	3.1 miles east of Tamarack	Aitkin	46.62958	-93.06663
8	E	Gulf of Mexico	Mississippi Headwaters–St. Croix	5.8 miles south of Solana	Aitkin	46.40021	-93.18063
9	E, I	Gulf of Mexico	Mississippi Headwaters–St. Croix	5.3 miles east of Malmo	Aitkin	46.34380	-93.40980
10	E, I	Gulf of Mexico	Mississippi Headwaters–St. Croix	8.1 miles SE of McGrath	Aitkin	46.17823	-93.12886
11	A, T	Gulf of Mexico	Mississippi Headwaters–St. Croix	6.3 miles NW of Ogilvie	Mille Lacs	45.87798	-93.53894
12	A, L	Gulf of Mexico	Mississippi Headwaters–St. Croix	6.1 miles SE of Ogilvie	Kanabec	45.75971	-93.35440
13	A, B, I, L, T	Gulf of Mexico	Mississippi Headwaters–St. Croix	4.4 miles east of Cambridge	Chisago	45.58702	-93.13554
14	A, B, L, T	Gulf of Mexico	Mississippi Headwaters–St. Croix	0.6 miles south of Forest Lake	Washington	45.27010	-92.98671
15	A, B, I	Gulf of Mexico	Mississippi Headwaters–St. Croix	1.9 miles SW of Pine Springs	Ramsey	45.02075	-92.98696
16	B, I, Q, T	Gulf of Mexico	Mississippi SE–Minnesota	1.3 mile south of Excelsior	Carver	44.88586	-93.55624
17	I, S, T	Gulf of Mexico	Mississippi SE–Minnesota	1.3 miles SW of St Bonifacius	Hennepin	44.89096	-93.76424
18	A, B, I, L, N, O, T	Gulf of Mexico	Mississippi SE–Minnesota	3.7 miles south of Cleveland	Le Sueur	44.27264	-93.84466
19	A, B, M, O, Q, T	Gulf of Mexico	Mississippi SE–Minnesota	0.7 miles east of Elysian	Le Sueur	44.20035	-93.66045
20	A, O	Gulf of Mexico	Mississippi SE–Minnesota	2.1 miles east of Lemond	Steele	43.99211	-93.34080
21	A, O	Gulf of Mexico	Mississippi SE–Minnesota	3.1 miles NW of Ellendale	Steele	43.89390	-93.35684
22	A	Gulf of Mexico	Des Moines–Minnesota	4.5 miles east of Ceylon	Martin	43.52760	-94.54164
23	A	Gulf of Mexico	Des Moines–Minnesota	1.3 miles NE of Sherburn	Martin	43.66458	-94.70638
24	A	Gulf of Mexico	Des Moines–Missouri	0.6 miles NW of Worthington	Nobles	43.62178	-95.60742
25	D	Gulf of Mexico	Mississippi Headwaters–Minnesota	1.9 miles NE of Bird Island	Renville	44.78574	-94.86616
26	I, L	Gulf of Mexico	Mississippi Headwaters–Minnesota	2.1 miles south of Spicer	Kandiyohi	45.20432	-94.95229
27	J, K, O, Q, R, V	Gulf of Mexico–Hudson Bay	Minnesota–Red River of the North	1.2 miles NW of Browns Valley	Traverse	45.60774	-96.85154
28	O	Gulf of Mexico–Hudson Bay	Minnesota–Red River of the North	1.2 miles north of Clinton	Big Stone	45.47714	-96.43030
29	O	Gulf of Mexico–Hudson Bay	Minnesota–Red River of the North	1.1 miles west of Chokio	Stevens	45.57690	-96.19458
30	A, T, I	Gulf of Mexico	Mississippi Headwaters–Minnesota	4.4 miles NE of Farwell	Douglas	45.80631	-95.56859
31	B, E, I, T	Gulf of Mexico	Mississippi Headwaters–Minnesota	5.4 miles SE of Millerville	Douglas	46.03055	-95.46236
32	E	Gulf of Mexico–Hudson Bay	Minnesota–Red River of the North	4.6 miles south of Battle Lake	Otter Tail	46.21340	-95.71563
33	A, E, F, I	Gulf of Mexico–Hudson Bay	Mississippi Headwaters–Red River of the North	4.9 miles NE of Solway	Beltrami	47.58515	-95.08841
34	I	Gulf of Mexico–Hudson Bay	Mississippi Headwaters–Red River of the North	9.6 mile NW of Turtle River	Beltrami	47.68379	-94.89928
35	A	Gulf of Mexico–Hudson Bay	Mississippi Headwaters–Red River of the North	3.6 miles west of Tenstrike	Beltrami	47.67372	-94.74804
36	A, E	Gulf of Mexico–Hudson Bay	Mississippi Headwaters–Red River of the North	2.0 miles south of Blackduck	Beltrami	47.70381	-94.54566
37	C, I	Hudson Bay	Red River of the North–Lake of the Woods	11.1 miles NW of Waskish	Beltrami	48.29927	-94.63743
38	C, I	Hudson Bay	Red River of the North–Lake of the Woods	3.2 miles east of Salol	Roseau	48.85534	-95.50156

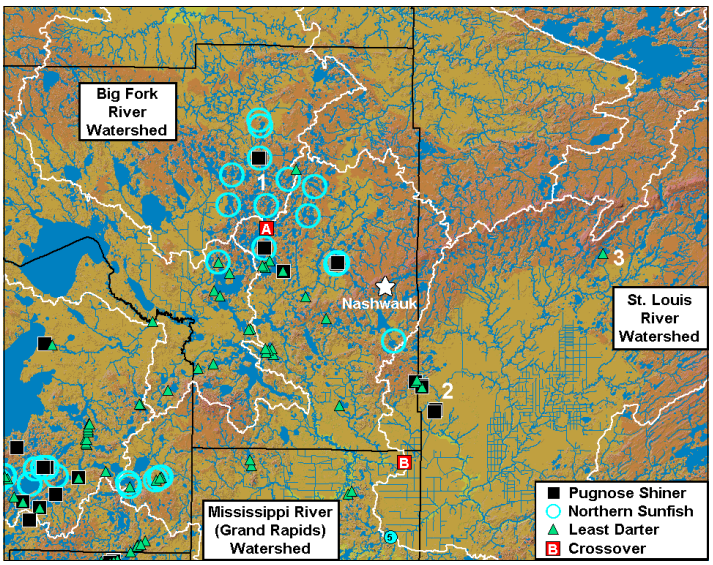

Figure 9. Primary crossovers A and B.

cies associate of Brook (*Salvelinus fontinalis*) and Brown trouts (*Salmo trutta*), but can persist in marginal trout streams and recovering (i.e., abandoned) coldwater ditches. The Mottled Sculpin and the Pugnose Shiner were the only two sensitive species also associated with secondary crossovers (i.e., 33 and 17, respectively). Seven of the 17 remaining species are associated with both primary and secondary crossovers and ten are restricted to secondary. The Yellow Bullhead (*Ameiurus natalis*) and Banded Killifish (*Fundulus diaphanus*) (Figure 8) may be the masters at scaling divides, occurring at 24 and 22 of the 48 crossovers, respectively.

The 48 crossovers include 20 on continental basin divides (i.e., Gulf of Mexico–Hudson Bay: 17; and Gulf of Mexico–Gulf of St. Lawrence: 3). The remaining 28 crossovers involve major drainage divides (i.e., Mississippi River Headwaters–St. Croix River: 10; Mississippi River Headwaters–Minnesota River: 7; Mississippi River Southeast–Minnesota River: 6; Des Moines River–Minnesota River: 2; Des Moines River–Missouri River: 1; and Red River–Lake of the Woods: 2) (Table 2). Primary crossovers associated with the greatest number of species involve continental divides at letters G with ten fishes and H with seven (Figure 6). High species numbers associated with secondary crossovers include one continental divide at number 27 with six species and two on drainage divides at 18 with seven and 19 with six.

This article will focus on primary crossovers involving continental divides (Figures 9, 11, and 14). Again these

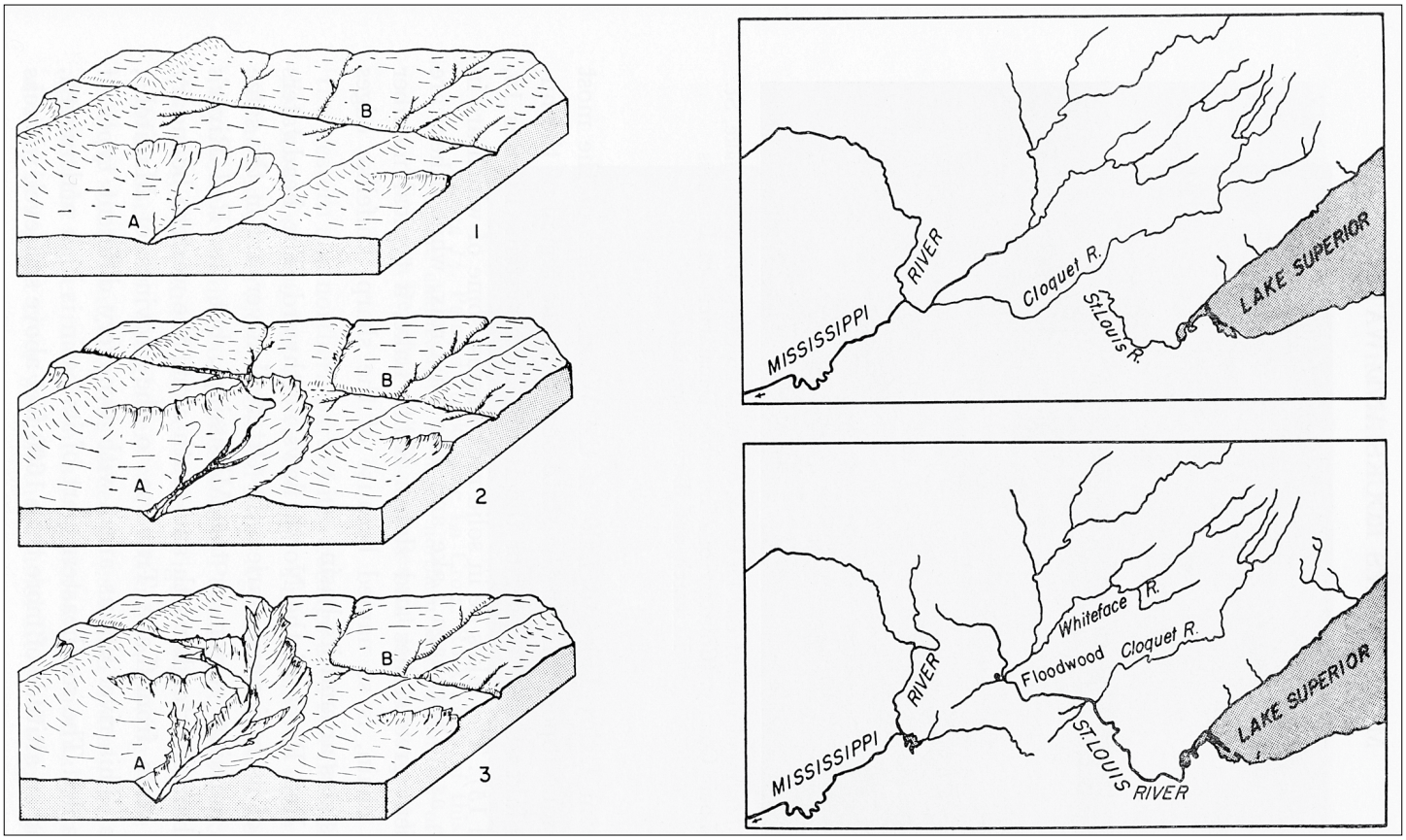

Figure 10. LEFT. Diagrams illustrating stream piracy: (1) The tributaries at *A* are advancing by headward erosion toward the valley of stream; (2) The stream *B* has been beheaded or captured and its headwaters are diverted to the pirate stream *A*; (3) The valley of A is extended and deepened. RIGHT. Maps showing the drainage changes of the St. Louis and Mississippi rivers: ABOVE, before stream capture; BELOW, after capture and diversion (Schwartz and Thiel, 1963).

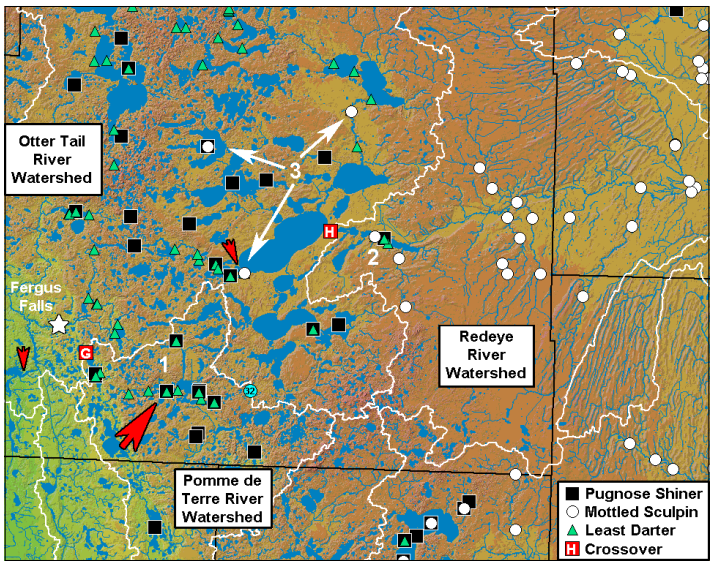

Figure 11. Primary crossovers G and H.

connections were identified from a "bread crumb" trail of sensitive species occurrences. One caveat that must be emphasized is surveys targeting these species amount to a miniscule fraction of the effort devoted to game species. Filling the data holes will not only refine this preliminary effort, but also contribute to the knowledge and status and habitats of rare and sensitive fishes.

Figure 9 illustrates crossovers on two different continental divides in northeastern Minnesota. Crossover A involves the Gulf of Mexico drainage via the Mississippi River and the Hudson Bay drainage via the Rainy River. Crossover B spans the drainages of the Gulf of Mexico via the Mississippi River and the Gulf of St. Lawrence via Lake Superior. Number 1 on the map indicates the location of Cameron Lake (Itasca County) where Pugnose Shiners occur at one of only two known localities in the Rainy River–Lake of the Woods drainage. Northern Sunfish are also restricted to only this portion of the Big Fork River watershed. Both species exhibit a wide—though spotty—distribution in the Mississippi Headwaters drainage. Yellow Bullhead and Banded Killifish (Figure 8) also shared an affinity for this crossover.

Numbers 2 and 3 on Figure 9 show the only known occurrences for Pugnose Shiners and Least Darters in the Lake Superior drainage. The cluster at 2 includes Long and Floodwood lakes and Floodwood River (St. Louis County). Number 3 is Ely Lake. Crossover B appeared to be the logical vector for these species, however, when I later stumbled into the discipline of geology I became aware of another likely route created from stream capture (Figure 10) through Savanna Portage State Park at secondary crossover 5 (Schwartz and Thiel 1963). I initially overlooked this connection as a primary crossover because only Spottail Shiner (*Notropis hudsonius*), which is a bait species, exhibited a likely link. At one time the Cloquet River belonged to the Mississippi River flowing through what eventually became the state park. However, headwater cutting of the much shorter St. Louis River bisected the Cloquet and diverted it to Lake Superior. Native Americans and fur traders used the portage as a route from the Great Lakes to the Mississippi River via the East and West Savanna rivers. In the early 1900s, one of the dredges used to dig the Panama Canal was brought here in an unsuccessful attempt to connect the two rivers for commercial navigation, but the ditch and dredge spoil banks remain visible today along the portage trail.

Figure 11 is at the opposite side of the state and displays primary crossovers G and H between the Gulf of Mexico–Hudson Bay basins. Both involve the Otter Tail River, which today is part of the Red River of the North drainage. The Otter Tail not only contains several species not found elsewhere in the drainage, but also by far is the most diverse. Crossover G exhibited the greatest cluster of species at any connection (i.e., Bowfin *Amia calva,* Cisco *Coregonus artedi,* Rainbow and Least Darter, Banded Killifish, Northern Hog Sucker, Longnose Gar *L. osseus*, Central Stoneroller *Campostoma anomalum*, Pugnose Shiner *Notropis anogenus*, and Weed Shiner *N. texanus*). Graf (1997) hypothesized that this was the result of another stream capture event based on both mussel and fish fauna, which far more resemble communities present in the Minnesota River drainage. The Otter Tail's original path is believed to have followed the present day Pomme de Terre River to the Minnesota River, but was later captured by the Red River of the North.

The occurrences clustered around number 1 on the map show all records for Pugnose Shiner and Least Darter which are restricted to the headwaters of the Pomme de Terre River watershed. Both species are widespread in the upper Otter Tail and Pelican river systems east and north of Fergus Falls. Crossover G appears to be the most likely connection for these species and also the Weed Shiner. However, secondary crossover 32 could be an alternate possibility even though Cisco was the only species that exhibited a nearby link to this route.

The large red arrow on the map is the only extant population of Rainbow Darters known in the Pomme de Terre watershed (Figure 12). The other population, near Appleton (approximately 70 air miles south), now presumed extirpated, has not been collected since 1954. The small red arrows identify the reach of the Otter Tail River where Rainbow Darters occur from the outlet of Otter Tail Lake to the head of Orwell Reservoir and represent the most northwestern periphery of the species' range (Figure 13). NANFA Fellow Ray Katula has kept all Minnesota popula-

Figure 12. Male and female Rainbow Darter (Pomme de Terre River, Otter Tail County, MN)

tions of Rainbow Darters except the Pomme de Terre. In 2012 he described the western populations (i.e., Minnesota drainage and Otter Tail River) as more stippled and less colorful than disjunct populations in eastern Minnesota (Katula 2012). His article included a summary of Kimberly Strand's research (formerly, University of Minnesota) who studied Rainbow Darter morphology of preserved specimens in the James Ford Bell Museum of Natural History fish collection. The following is an excerpt of her quote:

> The Ottertail River population does show unique characteristics including: higher number of rays on the second dorsal fin; lower number of scales around the caudal peduncle, but similar to the Lake Phalen population; the lowest average number of scales above the lateral line; on average the number of pored lateral line scales were the lowest in all populations studied; and the number of unpored scales one of the highest. Other populations do show potential for a variety of unique characteristics; however more samples are needed from most drainages for statistical purposes.

Figure 13. Male (top) and female Rainbow Darter (Otter Tail River, Otter Tail County, MN).

Crossover H (Figure 11) was second in the number of species associated with a connection (i.e., Bowfin, Cisco, Mottled Sculpin, Least Darter, Banded Killifish, Pugnose Shiner and Weed Shiner). The Otter Tail River appears to be the source of Pugnose Shiners and Least Darters in the Leaf Lakes (Otter Tail County) at number 2 and the only

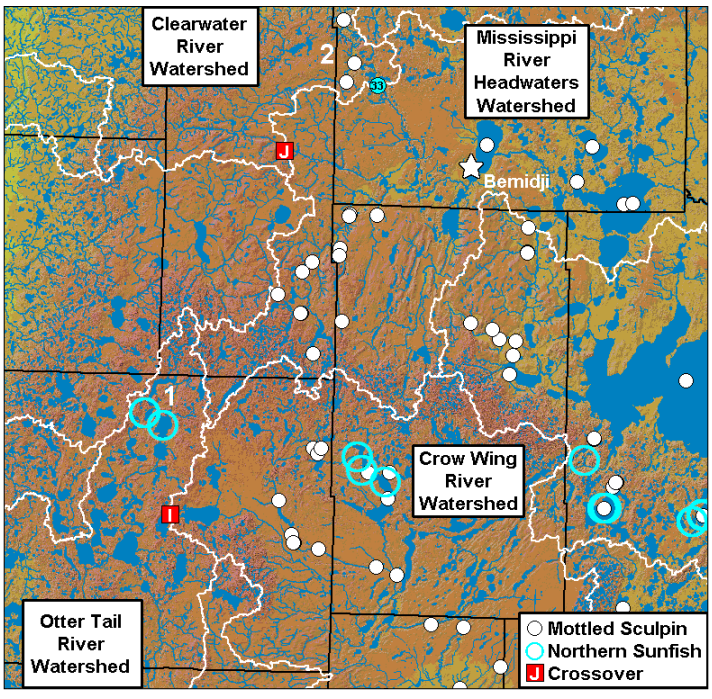

Figure 14. Primary crossovers I and J.

occurrences in the Redeye River watershed (Mississippi Headwaters drainage). Number 3 shows all the records of Mottled Sculpin in the Otter Tail watershed and this species probably also used crossover H from the Redeye River watershed.

The map in Figure 14 at number 1 shows the only localities for Northern Sunfish in the Red River of the North drainage (i.e., Little Bemidji and Many Point Lakes, Becker County). The nearest known populations in the Mississippi Headwaters drainage are in Island and Potato lakes (Hubbard County) and crossover I appears to be the likely route between the Crow Wing and Otter Tail watersheds. Central Stonerollers may have followed the same path as Northern Sunfish while Weed Shiners probably used this as this route in reverse to invade the headwaters of the Crow Wing River watershed.

Number 2 shows the only occurrences for Mottled Sculpins in the Clearwater River watershed (Red River of the North drainage) possibly passing through crossover J where the Yellow Bullhead and Banded Killifish may have also followed the same path. However, these species and Cisco could have also used crossover 33.

One last time I must emphasize these results are extremely preliminary and I expect further study will rule out some crossovers while at the same time identifying additional crossovers not yet considered. My hope is that this effort will eventually be used as a checklist to aid in a greater understanding of the distribution of Minnesota fishes.

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