ACROSS THE GREAT DIVIDE: FISH MOVEMENTS BETWEEN THE GREAT LAKES AND MISSISSIPPI RIVER BASINS AT PORTAGE, WISCONSIN

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If you're fascinated by the wonderful variety of fishes found across North America (why else would you be reading this?), it's hard not to be interested in biogeography, the study of the distribution patterns of plants and animals and the processes that determine these patterns. For freshwater fishes, one of the key questions in biogeography is if and how various species have been able to move from one river basin to another. Although the headwaters of two bordering basins may be very close as the crow flies, their mouths could be at different ends of the continent, and moving from one to the other via water would require traveling many miles downstream out of one basin and then many miles upstream into the other, often through long stretches of unsuitable habitat. Consequently, adjacent river basins may have very different fish faunas with little or no overlap in species composition despite close proximity and similar environmental conditions.

Yet, fish do sometimes move directly from one basin to the other through adjacent headwaters without the aid of people, resulting in these basins having multiple species in common and occasional genetic exchange. Typically, this type of fish movement takes place in mountainous areas via "stream capture" caused by erosion and landslides that divert a small stream from one basin into the other and in flatter areas via direct but temporary water connections across low-lying divides during periods of high water. Temporary connections are often a feature of northern regions shaped by the most recent ice ages, where past glaciation has steam-rolled the landscape and sometimes resulted in poorly defined wetland boundaries between watersheds.

Photos by John Lyons.

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THE PORTAGE CONNECTION

An important temporary connection between the Mississippi River Basin and the Great Lakes Basin was, until 73 years ago,

Figure 1. The Wisconsin River near Portage.

Figure 2. The Fox River near Portage.

Figure 3. Map of Wisconsin showing major rivers, lakes, and locations mentioned in the text.

Figure 4. The levee at Portage, started in the 1890s and finalized in the 1930s, which prevents flooding from the Wisconsin River from entering the city and the nearby Fox River.

Figure 5. The Portage Canal, photographed in 2023, linked the Wisconsin and Fox rivers from the 1850s until 1951. The canal, just under two miles in length, is now blocked at the Wisconsin River end, located just behind the view in this photo, but still connects with the Fox River.

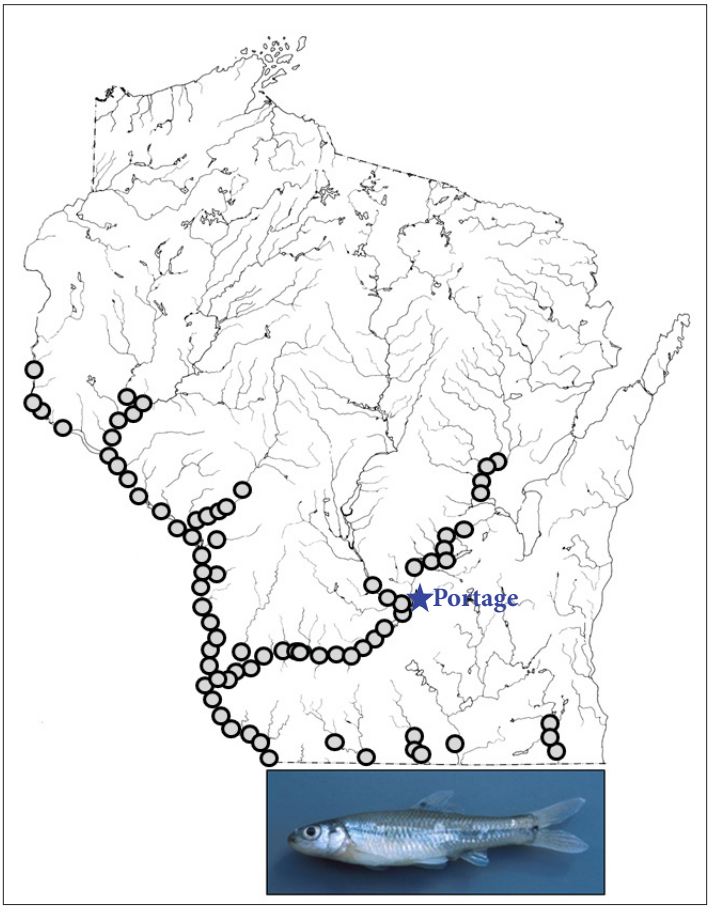

Figure 6. An example of a fish species distribution pattern, for the Bullhead Minnow, that suggests a colonization of the Great Lakes Basin from the Mississippi River Basin via the Portage connection.

found at the small city of Portage in south-central Wisconsin. Here, the mainstem of the Wisconsin River (Figure 1), a major tributary of the Mississippi River, passes about a mile from the headwaters of the Fox River (Figure 2), a major tributary of Green Bay and ultimately Lake Michigan (Figure 3). This area is flat and swampy and appears to have long served as a route for fishes to move between the two basins. The Wisconsin River is situated a few feet higher in elevation than the Fox River, and there are historical accounts of water from the Wisconsin flowing directly into the Fox during floods, an obvious conduit for fishes to move across the divide (Lyons et al. 2000). This flood diversion was a regular event until the first levees were built near Portage in the 1890s and continued sporadically during the largest floods until the levees were raised and strengthened in the 1930s (Figure 4).

The close connection between the Wisconsin and Fox rivers was the reason Portage was founded and given its name. For thousands of years, Native Americans would carry their canoes at this spot when moving between the two river systems. The early French explorers Joliet and Marquette came up the Fox River from Green Bay and first entered the Mississippi River by this route in the 1600s and early 1700s. In the 1850s, the crossover had become important enough for travel and commerce that a canal with locks of almost two miles in length was constructed so that boats could move directly between the two rivers (Figure 5). At about this same time, railroads became widespread in Wisconsin and reduced the demand for water routes to carry people and goods within the state, and Portage never became the transportation hub that city residents had hoped. But the canal remained operational until it was finally closed and sealed off from the Wisconsin River in 1951. In its nearly 100 years of existence, many fish undoubtedly used the canal to move between the Wisconsin and Fox rivers (Becker 1983).

FROM THE WISCONSIN RIVER TO THE FOX RIVER

At least 37 fish species may have colonized part of the Great Lakes Basin from the Mississippi River Basin by crossing over at Portage from the Wisconsin River into the Fox River (Lyons and Schmidt 2022). The evidence for this consists of a broad distribution of these species in the Mississippi River Basin including the Wisconsin River near Portage combined with a more localized distribution in the Great Lakes Basin, often limited to just the Fox River watershed and perhaps a few other nearby tributaries to Green Bay and adjacent Lake Michigan.

For instance, the Bullhead Minnow *Pimephales vigilax* is ubiquitous in the larger rivers of the Mississippi River basin including the Wisconsin River near Portage (Figure 6). However, it is absent from the entire Great Lakes Basin except for the Fox River and its largest tributary the Wolf River, both in Wisconsin, despite the presence of apparently suitable large-river habitats elsewhere in the Great Lakes Basin in Wisconsin, Michigan, Indiana, Ohio, and Ontario. This suggests that the Bullhead Minnow crossed over from the Wisconsin River to the Fox River at Portage relatively recently or at least within the previous 6,000 years. That was when the last of the once multiple post-glacial (i.e., beginning about 12,000 years ago) permanent connections between the Mississippi River Basin and the Great Lakes Basin, which occurred near present-day Chicago between the upper Illinois River and Lake Michigan, finally closed (Bailey and Smith 1981). If Bullhead Minnow had used the Chicago or other earlier connections, they would be expected to be far more broadly distributed within the Great Lakes Basin today.

As another example, the Western Sand Darter *Ammocrypta clara* is also found widely within the larger rivers of the Mississippi River Basin including the Wisconsin River, but it occurs in the Great Lakes Basin only in the Wolf River in Wisconsin and in the Menominee River, another Green Bay tributary on the border of Wisconsin and Michigan, again despite apparently suitable habitat elsewhere in the Great Lakes Basin (Figure 7). The population in the Menominee River occurs upstream of two dams that are impassable to upstream fish movement and that have been in place since the early 1920s, indicating that the colonization of the Great Lakes Basin by this species must have occurred more than 100 years ago but probably less than 6,000 years ago.

FROM THE FOX RIVER TO THE WISCONSIN RIVER?

There is little dispute that many Mississippi River Basin fishes used the Portage connection to gain access to the Great Lakes Basin (Becker 1983; Lyons et al. 2000; Lyons and Schmidt 2022). But did the opposite also occur: did some Great Lakes Basin fishes use the connection to colonize the Mississippi River Basin or at least the Wisconsin River watershed? The evidence for this would be a

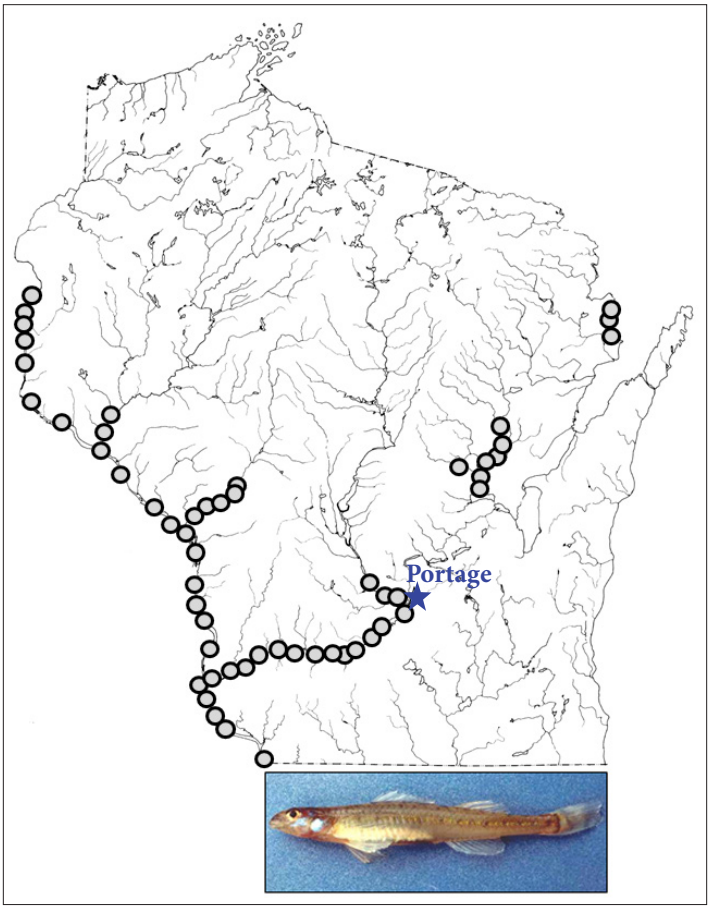

Figure 7. Another example of a fish species distribution pattern, for the Western Sand Darter, that suggests a colonization of the Great Lakes Basin from the Mississippi River Basin via the Portage connection.

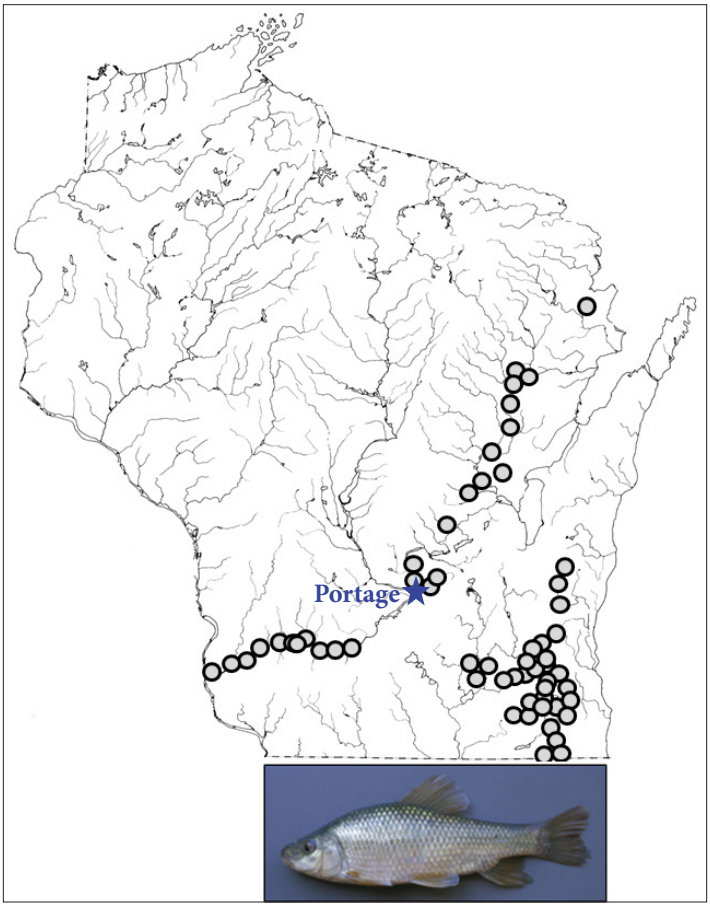

Figure 8. An example of a fish distribution pattern, for the Lake Chubsucker, that suggests a colonization of the Wisconsin River watershed from the Fox River via the Portage connection.

broad distribution in the Fox River watershed near Portage and elsewhere in the Great Lakes Basin and a more limited distribution in the adjacent Wisconsin River and points downstream. To our knowledge, no one has really considered this question, but as we have studied the biogeography of Wisconsin fishes, we have wondered whether this movement may have occurred for a few species. Let's delve into this in more detail for the four species that are most likely.

Lake Chubsucker *Erimyzon sucetta* (Figure 8):

Lyons and Schmidt (2022) felt that the Lake Chubsucker had colonized the Fox River from the Wisconsin River, but in doing more collecting and examination of distribution records in both systems, we are now not so sure. This species occurs in the upper part of the Fox River watershed and its major tributary the Wolf River and also elsewhere in the Great Lakes Basin in Wisconsin, Michigan, Indiana, Ohio, and Ontario. However, it is uncommon and localized in the Wisconsin River downstream of Portage. Although Lake Chubsucker is widespread in the Mississippi River Basin in the Rock River and Fox-Illinois River drainages in southeastern Wisconsin, these systems enter the Mississippi River in central Illinois far south of Wisconsin. Other than the Wisconsin River, there are no other records of established Lake Chubsucker populations in the Mississippi River Basin upstream from the Rock River watershed in northwestern Illinois (Metzke et al. 2022), which enters the Mississippi River more than 120 river miles downstream of the mouth of the Wisconsin River. We attribute a 2012 record of a single Lake Chubsucker in the mainstem of the Mississippi River about 10 miles downstream from the mouth of the Wisconsin River to a stray from the Wisconsin River. While we cannot rule out the possibility that the Lake Chubsucker swam up the Mississippi River mainstem from the Rock River to colonize the lower part of the Wisconsin River or that historically there was a more continuous distribution of Lake Chubsucker between the mouth of the Rock River and the mouth of the Wisconsin River, a simpler explanation is that the species moved from the Fox River into the Wisconsin River at Portage and then was carried or swam with the current downstream.

Blackstripe Topminnow *Fundulus notatus* (Figure 9):

Like Lake Chubsucker, Lyons and Schmidt (2022) considered Blackstripe Topminnow to have moved from the Wisconsin River into the Fox River, but now we think that the opposite may have occurred. The Blackstripe Topminnow is common in the upper Fox River watershed and in other areas of the Great Lakes Basin in Wisconsin, Michigan, Indiana, Ohio, and Ontario, but present at only a few scattered spots in the Wisconsin River watershed downstream of Portage. The Blackstripe Topminnow is widespread in the Rock River and Fox-Illinois River drainages, but except for the Wisconsin River it is unknown in

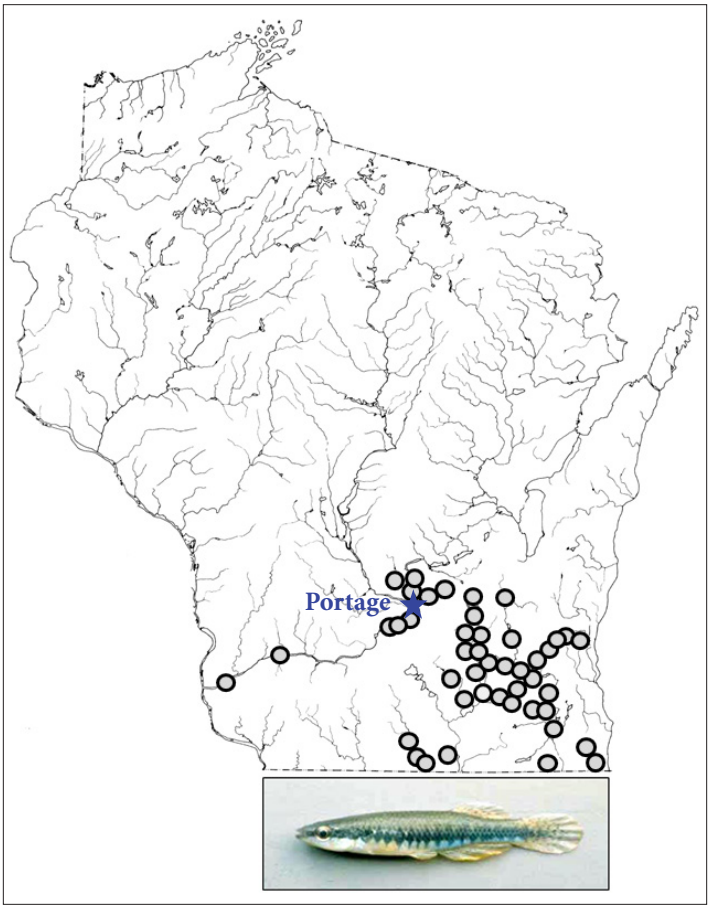

Figure 9. Another example of a fish distribution pattern, for the Blackstripe Topminnow, that suggests a colonization of the Wisconsin River watershed from the Fox River via the Portage connection, or, alternatively, of a human introduction from the Fox River into the Wisconsin River via a bait-bucket release.

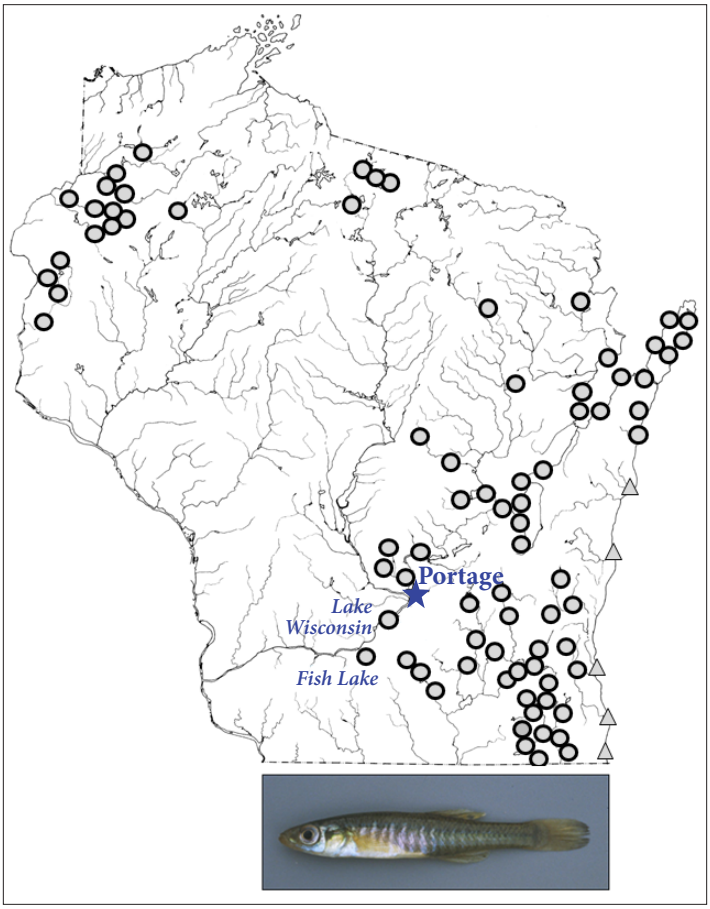

Figure 10. A fish distribution pattern, for the Western Banded Killifish (circles), that suggests a bait-bucket release for creating the only Wisconsin River drainage populations in Lake Wisconsin and maybe in Fish Lake, the killifish possibly originating from the nearby Fox River. (Triangles denote Eastern Banded Killifish.)

the upper Mississippi River Basin upstream of the Apple River in northwestern Illinois (Metzke et al. 2022), which enters the Mississippi River about 50 miles downstream of the mouth of the Wisconsin River. Like Lake Chubsucker, the simplest explanation for this pattern is that Blackstripe Topminnow entered the Wisconsin River at Portage and moved downstream, although the shorter distance from the Apple River to the Wisconsin River makes upstream movement or a more contiguous historical distribution in the Mississippi River more plausible for Blackstripe Topminnow.

Unlike Lake Chubsucker, which is an inconspicuous species that hides within aquatic vegetation and can be difficult to capture even in targeted surveys, the Blackstripe Topminnow swims in relatively obvious aggregations in open water near the surface and can be caught easily with dip nets or small seines. In the Fox River near Portage, Blackstripe Topminnows can be observed at almost any point along the stream. They and other larger topminnows and killifishes are also known to be sometimes captured and used as bait by anglers. This suggests that perhaps Blackstripe Topminnows were moved from the Fox River into the Wisconsin River via releases from bait buckets. The Wisconsin River near Portage is very popular for fishing, so this idea is conceivable. However, we have not found Blackstripe Topminnow in many nearby lakes and smaller rivers also popular for fishing, making this option perhaps less likely than a direct movement of fish from the Fox River, either through the canal or during a flood.

Western Banded Killifish *Fundulus diaphanus menona* (Figure 10):

In contrast to Blackstripe Topminnow, for Western Banded Killifish, the bait bucket option is perhaps the most likely scenario for movement from the Fox River into the Wisconsin River. This species has a unique distribution pattern. It is widespread in eastern Wisconsin throughout much of the Lake Michigan Basin including the upper Fox River watershed and much of the Mississippi River basin in the Rock and Fox-Illinois River drainages and extending into northeastern Illinois. It is also known from the Great Lakes Basin in Illinois, Michigan, Indiana, Ohio, and Ontario. Elsewhere in the Mississippi River Basin it is locally common in Minnesota and in northern Wisconsin, there in the upper St. Croix River and Chippewa-Flambeau River drainages. However, except for two populations downstream of Portage, it is completely absent from the Wisconsin River watershed, which is located between the northern and eastern portions of Wisconsin. No other fish species has this "gap" in distribution, which cannot be readily explained.

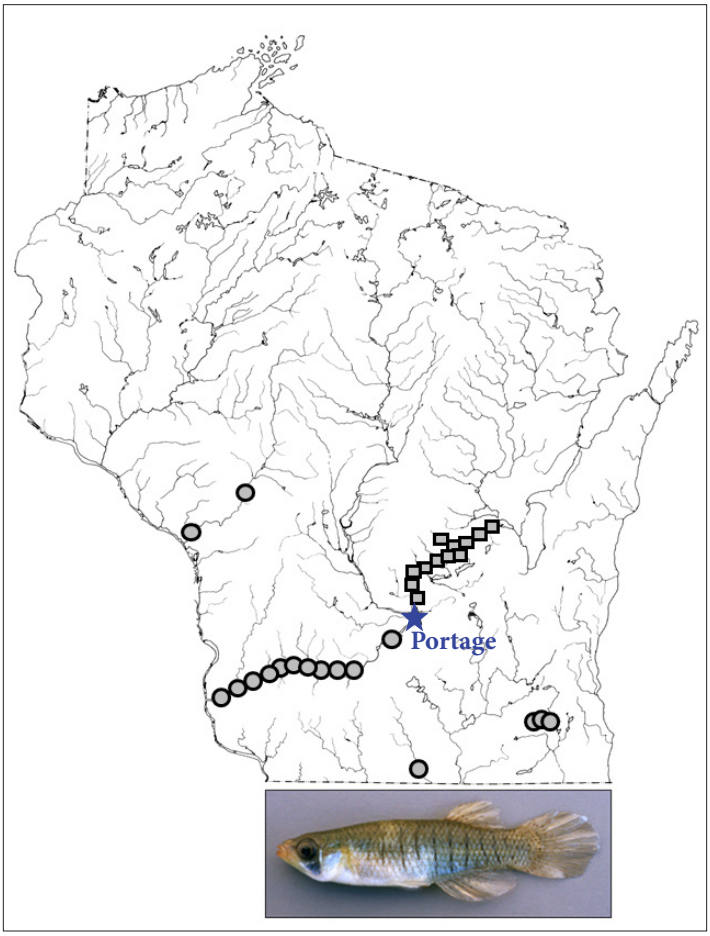

Figure 11. A fish distribution pattern, for the Starhead Topminnow, that cannot be easily explained. If the recently discovered Fox River populations (squares) originated within the last 25 years, then a bait-bucket or aquarium release seems possible as a source, but the rarity of the species in Wisconsin makes this improbable. If the species has long been present in the Fox River but was missed up until recently, then the Portage connection may have allowed movement between the Fox and Wisconsin rivers, but the direction of the movement is uncertain.

One of the Wisconsin River records for Western Banded Killifish is from Lake Wisconsin, an impoundment of the Wisconsin River located about 10 miles downstream of Portage formed by the Prairie du Sac Dam, which dates from 1914 and is impassable to fish moving upstream. The species was first collected from Lake Wisconsin in 2009 and occurs in three nearby bays in the middle portion of the lake (Lyons et al. 2022). It has not been found elsewhere in the Wisconsin River despite extensive sampling over the last 100 years, including several surveys of Lake Wisconsin before 2009. It has not expanded its range within the lake since 2009 even though other bays both upstream and downstream appear to have suitable habitat, similar to where it currently occurs. Although we cannot be certain, we attribute the Lake Wisconsin population of Western Banded Killifish to a relatively recent and inadvertent introduction by anglers using it for bait. If the species had colonized the Wisconsin River naturally through the Portage connection sometime before it was closed in 1951 or if it had always been present in the Wisconsin River, we would expect it to be far more widespread in the Wisconsin River system. We would also expect that it would have been found before 2009. The upper Fox River is by far the closest and thus most likely source of Western Banded Killifish for bait.

The other Wisconsin River drainage record is from Fish Lake, located about 30 miles southwest of Portage and three miles from the Wisconsin River. Although it is in the Wisconsin River watershed, this lake does not have an inlet or outlet connecting it to the Wisconsin River or any other bodies of water. All fishes there today had to have either colonized soon after the glaciers receded when the lake did have water connections to other lakes and rivers, or they had to have been brought there much more recently by people. The first collection of Western Banded Killifish from the lake was in the early 1990s, although few surveys of the smaller fishes in the lake had been conducted before then and the species may have been present earlier. It is conceivable that the Western Banded Killifish has always been in the lake, but it is also plausible that the species is a relatively recent introduction by anglers, perhaps from the upper Fox River, one of the nearest sources. The lake is very popular for fishing. But it is certain that the Western Banded Killifish did not enter the lake on its own from the Wisconsin River in recent times.

Starhead Topminnow *Fundulus dispar* (Figure 11):

The origins of the Starhead Topminnow in the Wisconsin and Fox rivers are unclear. The species is rare in Wisconsin and listed as an endangered species in the state. Until quite recently, it was thought to be found only in four areas in Wisconsin, all in the Mississippi River basin: localized portions of the Rock River, Fox-Illinois, and Black River watersheds, and a more extensive stretch of sloughs and backwaters along the Lower Wisconsin River below the Prairie du Sac Dam. The Lower Wisconsin River is considered the stronghold of the species in the state. Since 2018, the first three authors have successfully reintroduced Starhead Topminnows into their historical range in the Wisconsin River upstream of the Prairie du Sac Dam (Lyons et al. 2021, 2022; Marshall et al. 2021). The Starhead Topminnow was not thought to occur in the Great Lakes Basin in Wisconsin although it is found in the Lake Michigan Basin of southern Michigan.

Recently, the fourth and fifth authors made the exciting and completely unexpected discovery that the Starhead Topminnow is currently widespread and thriving in the upper Fox River watershed. Their first collection was from 2005, and they have now found the species at multiple locations spanning over 45 miles of the Fox River downstream of Portage and over 10 miles up a tributary, the White River. The origin of Starhead Topminnow in the Fox River is a mystery with two potential explanations, neither completely satisfactory.

One possibility is that the Starhead Topminnow has long been present in the Fox River watershed and was simply missed in past surveys. But this explanation seems improbable to us. At present, Starhead Topminnows are common and easily observed at many places on the Fox River, and it seems that if their abundance and distribution had been similar in the past then they would have been captured in at least one of the many collections made in the upper Fox River drainage from the 1920s through 2004 (Greene 1935; Becker 1983; Lyons et al. 2000; Lyons and Schmidt 2022).

Perhaps they were much scarcer in the past and not nearly as likely to be encountered as now. But why would that be, and why have they apparently surged in numbers and extent in recent years?

The other possibility is that the Starhead Topminnow has been recently introduced into the Fox River from a population in the Mississippi River Basin, perhaps the closest one in the Lower Wisconsin River. In theory, the source could be an angler's bait bucket or a release by an aquarium hobbyist. However, neither explanation seems very plausible to us. Starhead Topminnows are quite rare in Wisconsin, illegal to possess, and too small and fragile to make good bait, so their collection, use, and spread by anglers strikes us as highly improbable. The species is somewhat popular among native-fish aquarium hobbyists, but again its scarcity and legal status suggest that few if any Wisconsinites would have ever collected it locally for their tanks. Wisconsin native-fish hobbyists do obtain fish from outside the state, so the species could have arrived from a region where it is more common. But that still presupposes that a hobbyist would have released their unwanted Starhead Topminnows in the Fox River. Not impossible but requiring an unlikely sequence of steps.

If the Starhead Topminnow has long been in the Fox River and was not introduced by people (the first possibility), then its distribution pattern does not unambiguously indicate whether it used the Portage connection to colonize the Fox River from the Wisconsin River of vice versa. The current distribution of Starhead Topminnow outside the Fox and Wisconsin rivers is too spotty to infer its direction of movement. Conceivably, it could have come up the Mississippi River from the south and into the Wisconsin River and then crossed over to the Fox River at Portage. The presence of Starhead Topminnow further upstream in the Mississippi River Basin in the Black River supports this option, but the nearest source population to the south would be in the Rock River watershed (Metzke et al. 2022), a long swim away. Conversely, Starhead Topminnows from Michigan could have moved along the Lake Michigan shoreline and into Green Bay and then up the Fox River to Portage. But that would entail a great journey within a large, cold, and generally unsuitable lake before even getting to the mouth of the Fox River, and then an upstream migration of over 150 miles to the upper Fox River. If we had to choose, we think that the Starhead Topminnow probably entered the Fox River from the Wisconsin River via the Portage crossover rather than the other way around, but we have doubts about both alternatives.

CONCLUSIONS

Understanding and reconstructing how current fish distributions came about, while fundamental to biogeography, is always a challenging process. And almost inevitably, human activities like canal building, bait-bucket transfers, and aquarium releases complicate the analysis. The Portage connection has played an important role in determining the current distribution of fishes in Wisconsin and more generally in their movement between the Mississippi River Basin and the Great Lakes Basin. However, the details of approximately when, how, and in what direction these movements took place for individual species are often uncertain. Yet, it is that very uncertainty and the detective work necessary to try and resolve it that is one of the appeals of the study of biogeography.

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