North America's Freshwater Fishes: Where They Came From, How They Got Here, and Why They Are Where They Are

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From cold Arctic rivers to warm subtropical streams, from majestic rivers like the Mississippi to small springs in the middle of deserts, fish can be found in North America just about anywhere there's relatively unpolluted water.[1] But where did all these fishes come from? Did they swim here from somewhere else? Or were they always here? Why are some species found in just one or two small locations, while others are widespread across the continent? (See page 14 for an analysis of two extreme cases.) These are the types of questions studied by zoogeographers, and the answers are usually a mosaic of geologic, climatic and biotic factors. One way to explain fish distributions is to imagine that these factors impose a series of "faunal screens" that "filter" the available fishes of the world down to those found at any given site on any given day (Fig. 1).

Continental Drift

The first and coarsest filter is continental drift, the theory that continents are not fixed and immovable, but forever drifting across the Earth's crust—"like leaves on a pond," to quote travel writer Bill Bryson (2003). North America is no exception. Over the millennia, North America has repeatedly merged and separated from other continents, alternately allowing and preventing the exchange of various fish groups.[2] Ancestors to North America's present day archaic or "fossil" fishes—lampreys, sturgeons, paddlefish, bowfin, and gars—hail from Pangaea, the supercontinent in which all the world's continents had been fused 180 million years ago. Forty or so million years later, while Pangaea was splitting into a northern landmass, Laurasia (the future North America, Europe and Asia), and a southern landmass, Gondwanaland (the future South America, Africa, India, Australia, and Antarctica), various modern freshwater fish groups began to develop. On Laurasia these consisted of what would later become today's pikes, mudminnows, pirate perch, trout-perch, cavefishes, and salmonids (salmon, trout, ciscoes, and whitefishes). Other fish families—most notably minnows, suckers and perches—arrived here via one (or both) land "bridges" that connected northern North America to Eurasia at various times across the Atlantic Ocean and the Bering Strait. Characins and other neotropical fishes began entering North America about 14 million years ago, when the uplift of Central America connected North and South America for the first time since their Pangaean days.

While continental drift explains the presence of several fish groups in North America, it does not explain their distribution patterns across the continent. For this we turn to the next faunal screen, Pleistocene glaciation.

[1] Fishless aquatic habitats in North America include high-altitude glacial lakes, desert playas (the flat-floored bottoms of undrained desert basins that can become shallow lakes), lakes with an unusually high salinity or pH, and extreme headwater streams usually above waterfalls.

[2] For much more detailed accounts of Noth American continental drift and its influence on the freshwater fish fauna, see Briggs (1986), and Matthews (1998: 202-235).

Pleistocene Glaciation

During this period, which began about 2.5 million years ago and ended (it is believed) about 10,000 years ago, as much as a third of North America was covered with glaciers. As glaciers advanced (grew) they killed just about everything in their path. As glaciers retreated (shrunk), they carved new lakes and rivers in the bedrock, rerouted some river systems,[3] and altered the land by widening or deepening river valleys and forming waterfalls, all of which had profound effects on fish distributions. In fact, it's glaciers that largely account for why most North American fish species are concentrated in the central and southeastern parts of the U.S. and fewer species are located in the north. The Mississippi Basin, for example, contains the richest fish diversity in North America because it served as a refuge and major center of fish evolution when glaciers covered points north.[4] In contrast, the Hudson Bay and North Appalachian parts of North America were fishless just 14,000-15,000 years ago; their fishes began moving in from the south once the ice started to melt. Such colonization is slow, depending largely on a geological process known as stream capture (defined and illustrated in Fig. 2.)

Whereas stream capture can facilitate the dispersal of fishes into new areas, our next faunal screen, zoogeographic barriers, prevents or limits it.

Zoogeographic Barriers

Depending on the species, barriers include waterfalls, harsh climates, heavily turbid or silted rivers, the ocean, canyons, and mountains. But zoogeographic barriers by no means suppress fish diversity; in fact, they usually increase it. Let's say a mountain starts to rise in the middle of the range of a fairly widespread species. Over time, the fish's population gets separated into two groups, one on each side of the mountain. With genetic interchange now impossible because of the mountain in between, the two populations follow separate evolutionary paths, undergo different genetic mutations, and eventually become two species. Zoogeographers have a name for this process: vicariance. (On a much larger scale, continental drift causes vicariance, too.) The distribution of fishes

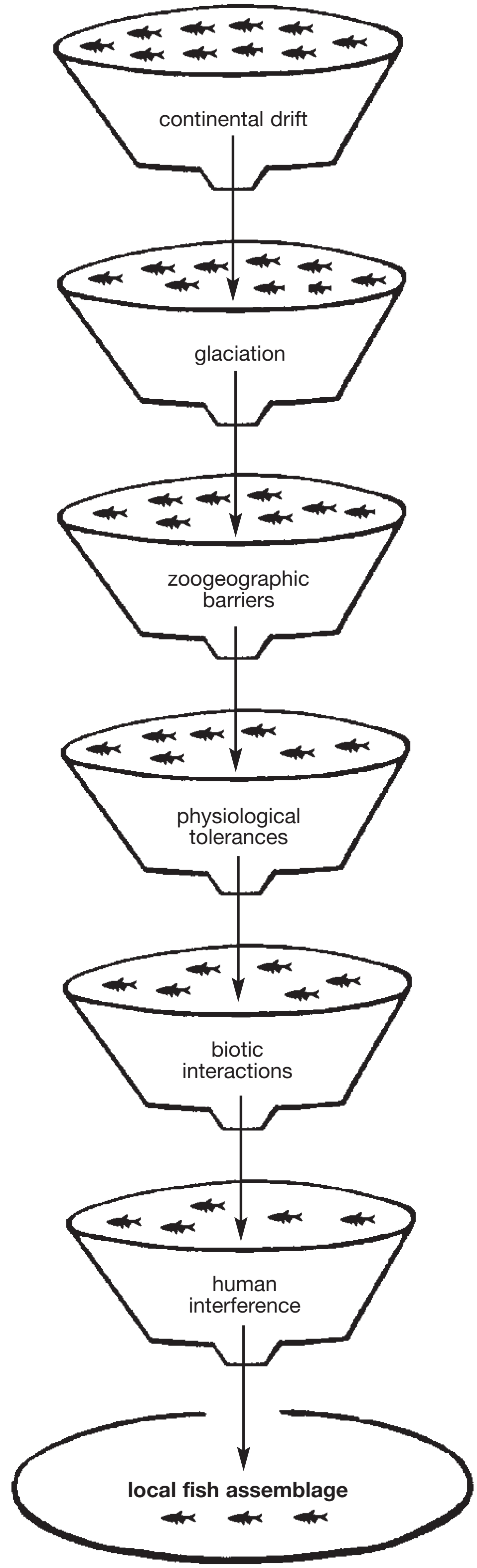

Fig. 1.
Hypothetical diagram showing how a series of "faunal screens" representing geologic, climatic, biotic, and anthropogenic (human-caused) factors "filter" out available fishes to form the present-day distribution of a local freshwater fish assemblage.

[3] For example, the upper Missouri River flowed north, presumably into Hudson Bay, before glaciation.

[4] Indeed, the Mississippi Basin has been called the "mother fauna" of North America and a "cradle of temperate freshwater fish diversity" (Burr and Mayden, 1992).

The Pike and the Pupfish: A Zoogeographic Comparison

The Northern Pike (*Esox lucius*) has the largest natural geographic range of any freshwater fish in North America (D. A. Neely, pers. comm.). It occurs in lakes, creeks, and small to large rivers from Labrador to Alaska south to Pennsylvania, Missouri and Nebraska, covering an area of approximately 11,130,000 sq km (4,297,629 sq mi).

In contrast, the Devils Hole Pupfish (*Cyprinodon diabolis*) has the smallest natural geographic range of any freshwater fish in North America—indeed, of any known vertebrate species in the world (Berra, 2001). The entire population of this inch-long fish feeds and breeds on a scant 6' x 10' limestone ledge along one side of Devil's Hole, a pool at the head of an underground water system in the Death Valley System of Ash Meadows, Nevada.

Why is the pike found over half of North America (51.5%) while the pupfish is confined to an area smaller than most bedrooms? The answer makes for an excellent case study in how climatic and geologic factors can influence the distribution—and creation—of fish species. In effect, both the pike and the pupfish are products of glaciers, though in entirely different ways.

The Northern Pike is a cold-adapted species, inhabiting Arctic drainages in Asia and Europe as well as North America. As glaciers advanced across northern North America, the pike sought refuge in at least two refugia, the southern Mississippian refuge and the northern Beringian refuge in parts of northwest Canada and Alaska. As the ice sheets retreated, the pike was able to recolonize most of northern North America from both the south and the northwest. The lack of major geographic barriers between the southern refuge and northern tributaries, coupled with the fish's role as a large predator capable of traversing long distances, also facilitated the northern pike's wide dispersal.

Unstable climatic conditions and the presence of geographic barriers prevented a similarly wide dispersal of fishes from occurring in the American West, including the area that's home to the Devils Hole Pupfish. As glaciers retreated, a drying trend occurred that caused glacier-fed lakes and large interconnected rivers to contract and disappear. Fishes were forced to seek refuge in small springs fed by groundwater (the trapped runoff of melting glaciers) and small streams fed by melting mountain snow and the occasional cloudburst. Literally unable to traverse mountains, western fishes could not disperse and recolonize new areas like their cousins to the north and east. Over the course of 12,000 to 20,000 years, the region's ancestral pupfish, now isolated in 10 populations, evolved to become 10 distinct separate species or subspecies. The most isolated of these populations was at Devil's Hole. Located at an elevation of 730 m (2395 ft), the highest point in Ash Meadows, the Devils Hole Pupfish lives in a fault fracture 15 m (49 ft) below the surface of the earth. The limestone ledge to which the species owes its entire tenuous existence is the only portion of Devil's Hole exposed to light.

in the eastern U.S., with its hundreds of darter and minnow species, is a complex combination of dispersal (fishes crossing barriers) and vicariance (barriers imposed on fishes).

Physiological Tolerances

A fish's physiological tolerances may also serve as a faunal screen. If the temperature, salinity, pH, and dissolved oxygen levels of a body of water are not within a fish's "comfort zone," it will choose not to live there or risk death if it does. Brook Trout, for example, like their water cold. Continental drift may have brought ancestral trout to North America, glaciation may have restricted them to the eastern United States, and various zoogeographic barriers may limit them to certain drainages, but it's their intolerance for water much above 55°F (13°C) that keeps them in the colder spring- and snow-fed streams within that drainage system.

Biotic Interactions

Biotic interactions with other animals provide another faunal screen. A fish will not be able to establish a permanent

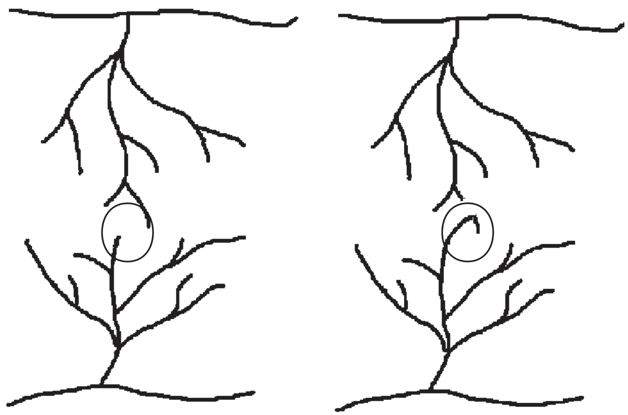

Fig. 2.
Stream capture (also known as stream piracy) is a geological process in which one stream erodes into another and "captures" the water in it (indicated in circles). Plants and animals are often exchanged when the two streams come in contact.

reproducing population in a body of water where it cannot compete for food, or too often *becomes* food to other species. What's more, biotic interactions often help explain the distribution of a fish within a body of water itself. In order to get enough to eat and not get in each other's way, fish species often partition themselves among different ecological niches, or microhabitats: deep vs. shallow, fast vs. slow, top vs. bottom, and so on.

Fish distribution is a dynamic process. Indeed, natural phenomena can happen at any time that move a fish from one location to another. Floods can move fish across drainages. Ducks can transport fish eggs on their feet. And folk tales of it "raining fishes" are often true; waterspouts can pick up small fishes and move them across land. Of course, physiological tolerances and biotic interactions will determine if a fish permanently survives its relocation.

Human Interference

Finally, there is one significant—though unnatural—factor in fish distributions. And that is us. Since the time of European settlement, humans have been proficient at moving fishes into areas where they do not belong, and preventing fishes from living in areas where they do. The result has been the introduction of numerous foreign (or exotic) fish species, almost always to the detriment of the native fauna; the homogenization of the continent's fishes through the release of indigenous fishes into areas outside their natural ranges; and the increasing rarity if not complete disappearance of countless fishes because of habitat destruction and modification. What took hundreds of millions of years and the movement of continents and glaciers to create, we have profoundly and irreparably messed up.

Literature Cited

Berra, T. M. 2001. *Freshwater fish distribution*. New York: Academic Press.

Briggs, J. C. 1986. Introduction to the zoogeography of North American fishes. *In*: Hocutt, C. H., and E. O. Wiley (Eds.). *The zoogeography of North American freshwater fishes*. New York: John Wiley and Sons.

Bryson, B. 2003. *A short history of nearly everything*. New York: Broadway Books.

Burr, B. M., and R. L. Mayden. 1992. Phylogenetics and North American freshwater fishes. *In*: Mayden, R. L. (Ed.). *Systematics, historical ecology, and North American freshwater fishes*. Stanford, Ca.: Stanford University Press.

Matthews, W. J. 1998. *Patterns in freshwater fish ecology*. New York: Chapman & Hall.