

THE ORIGIN OF WILLISTON FISH SPECIES

Since the entire upper Peace drainage basin was covered in ice during the last (Wisconsinan) glaciation, even the native fauna is made up of relatively recent immigrants. Although we know nothing about the pre-Wisconsinan fish fauna in the upper Peace system, it is clear from fossils found elsewhere that immediately before the last glaciation the North American fish fauna was made up essentially of modern species. For example, two species that are now widespread in British Columbia (the redbelt shiner and the largescale sucker) are known from early Pleistocene deposits in Idaho. Similarly, another B.C. species the brassy minnow is known from early Pleistocene deposits on the Great Plains. In addition, the longnose sucker, burbot, Arctic grayling, and slimy sculpin, occur in deposits found in the Yukon Territory that are about 60,000 years old. Consequently, the fishes of the pre-Wisconsinan Peace River probably were modern species. Presumably, however, these populations were either destroyed during the last glaciation or pushed into ice-free regions called glacial refugia.

Major refugia --- With the retreat of the ice, fish were able to disperse back into the upper Peace system from three major refugia --- the unglaciated regions south of the ice and west of the Continental Divide (the *Pacific* or *Columbia* Refugium), the unglaciated regions south of the ice and east of the Rocky Mountains (the *Great Plains* Refugium), and the unglaciated regions of the Yukon and Alaska (the *Bering* Refugium). Associated with each of these major refugia were smaller isolated regions that acted as minor refugia. For example, the Great Plains Refugium contained both upper Mississippi and upper Missouri tributaries. Although the two drainage systems are connected and, theoretically, fish could swim from one system to the other, the upper portions of these drainages were substantially isolated. Thus, for example, there is evidence of genetic divergence between Mississippi and Missouri populations of northern pike. Most of the

fish that entered the Peace system from the Great Plains Refugium probably dispersed from the western (Missouri) portion of the refugium. Nonetheless, at least three species (northern redbelly dace, finescale dace, and pearl dace) reached the lower Peace region from the eastern (Mississippi) portion of the refugium. Similarly, there is growing evidence for a minor refugium, separate from the Bering Refugium, in the Nahanni drainage system. An ice-free area in the Nahanni drainage would be well positioned geographically to contribute colonists to the upper Peace system by way of connections between the Finlay and Kechika rivers.

Two lines of evidence --- geographic distributions and genetic markers --- allow us to assign native fishes to one or more of these ice-free regions. For example, if the present distribution of a species includes only one of ice-free region, then that region probably is the source of the upper Peace populations. On the basis of present distribution, nine of the 21 native species in the upper Peace can be assigned to a single ice-free region. Seven species (mountain whitefish, bull trout, peamouth, northern pikeminnow, redbelly shiner, largescale sucker, and prickly sculpin) clearly evolved west of the Continental Divide and entered the Peace system from the Pacific Refugium. Similarly, two eastern North American species (brassy minnow and white sucker) reached the upper Peace from the Great Plains Refugium.

The remaining 12 species are more difficult to assign. Their distributions include more than one refugium and they could have survived in several ice-free regions. Presumably, such species were widely distributed before the last glaciation and that the advancing ice disrupted their ranges. Thus, fragments of once continuous distributions were left in more than one refugium. A consequence of this range fragmentation was the cessation of gene flow between fragments. Over time, geographic isolation and different selection pressures in different refugia led to genetic divergence. Later, as the ice retreated, these divergent forms were able to expand their ranges back into formerly

glaciated areas. These forms derived from different refugia are only slightly differentiated genetically and have no taxonomic status; however, they often differ in life-history traits and habitat use. Consequently, they are of some interest to fisheries managers and, with the advent of sensitive techniques for detecting genetic differences, it is now possible to reconstruct cases of postglacial dispersal from multiple refugia.

Slightly over half (57%) of upper Peace fishes could have entered the drainage from more than one source. The geographic distributions of six species (pygmy whitefish, lake chub, longnose dace, longnose sucker, burbot, and slimy sculpin) include the Pacific, Bering, and Great Plains refugia. With the exception of longnose dace, these are all cold-adapted species. Such species probably exploited the ephemeral drainage connections between major river systems that characterized the early stages of deglaciation. Interestingly, for three species (lake chub, longnose sucker, and slimy sculpin) there is evidence that the upper Peace is an area of contact and inter-mixing of populations from different refugia. The distributions of the other six species include only two potential refugia. Three species (lake whitefish, lake trout, and Arctic grayling) could have survived in either the Bering or the Great Plains refugia. For the upper Peace the evidence so far suggests that our lake trout are of Bering origin, our Arctic grayling at least partly of Nahanni origin, and our lake whitefish of Great Plains origin. The distributions of the remaining three species (rainbow trout, Dolly Varden, and Kokanee) include both the Pacific and Bering refugia. Again, there is genetic evidence that glaciation subdivided at least two of these species (rainbow trout and kokanee).

Postglacial dispersal --- The unglaciated portions of the Columbia River system were the main source of postglacial immigrants into the interior of British Columbia, and most radio carbon dates indicate that by about 15,000 BP (before present) the ice was retreating northward along the entire southern edge of the Cordilleran Ice Sheet. Details of ice-retreat in the interior of the province are complex, however, and ice-retreat was

strongly influenced by local topography and climate. Thus, the ice withdrew rapidly from most valleys but remained longer in highland areas. Rapid retreats sometimes isolated large blocks of stagnant ice in valleys while minor readvances blocked rivers and created large proglacial lakes.

In the central interior, the ice had withdrawn to the north of Prince George by about 10,000 BP; however, a later ice advance from the Cariboo Mountains blocked the middle Fraser River and ponded a large lake (Glacial Lake Prince George). Eventually this massive lake overflowed into the Crooked River (an upper Peace tributary). When the ice blocking the Fraser River withdrew, Glacial Lake Prince George re-established its southwards flow and quickly drained. Apparently this sequence of ice blocking the middle Fraser and ponding a large eastward draining lake was repeated at least twice during deglaciation. Presumably, these ephemeral connections between the Fraser and upper Peace systems provided fish of undoubted Pacific origin (e.g., rainbow trout, bull trout, mountain whitefish, peamouth, northern pikeminnow, redbelt shiner, largescale sucker, and prickly sculpin) with access to the upper Peace system. Interestingly, two other species (kokanee and Dolly Varden) appear to have reached the upper Peace from Pacific drainages by other routes. As far as is known, kokanee entered the upper Peace twice --- once into the upper Parsnip River (Arctic Lake) from the McGregor system (a Fraser tributary), and once into the upper Finlay River (Thutade Lake) from the Sustut system (a Skeena tributary).

For fish, the postglacial drainage connections between the Fraser and the upper Peace were not a one-way street. At least two fish of clear eastern origin (white sucker and brassy minnow) were able to colonize the upper Fraser system. Additionally, genetic markers indicate that upper Peace and Fraser populations of lake trout and lake whitefish are of Great Plains origin. The Peace Canyon stopped most of the Great Plains fish fauna. How, then, did a few species reach the upper Peace and, eventually, the

Fraser system? The simplest explanation is that these species reached the Peace system before the barrier existed and that other species arrived after the barrier formed.

Thirteen thousand years ago, a large proglacial lake (Glacial Lake Peace) occupied much of what is now the Peace drainage basin. This lake existed for several thousand years in a number of different stages with different drainage connections. During one of the early stages of Glacial Lake Peace, when the outlet drained southeast into the Missouri system, the Peace River Canyon was inundated. Consequently, species that reached Glacial Lake Peace before the canyon became a barrier could have dispersed upstream and into one of the stages of Glacial Lake Prince George. These glacial lakes and their interconnections must have been harsh environments: cold, turbid, and unproductive. One can imagine fish like lake trout, lake whitefish and, even, white sucker using such dispersal corridors; however, for the brassy minnow this explanation seems implausible. In the upper Peace, the brassy minnow is associated with small, boggy lakes and streams. It now occurs in such environments on both sides of the low divide between the Peace and Fraser systems at Summit Lake. Perhaps, at one time, such habitats were common on the benches on either side of the Peace River Canyon and this species somehow was able to circumvent the barrier. For now, however, the way the brassy minnow reached upper Peace drainages remains a mystery.

There is no unequivocal evidence that any species reached the upper Peace from the Bering Refugium; however, the northern Rocky Mountain Trench forms an obvious route whereby fish that entered the upper Liard system from the Yukon system could have dispersed into the upper Peace --- the headwaters of the Kechika (an upper Liard tributary) and the Finlay (an upper Peace tributary) interdigitate in Sifton Pass. So far, the best evidence for the use of the Kechika-Finlay dispersal route comes from Arctic grayling. There are allelic differences between grayling above and below the

Peace Canyon. Variant alleles in upper Peace populations are shared with upper Liard grayling, while common alleles in lower Peace grayling are shared with Great Plains grayling and absent in the upper Peace. Similarly, some upper Peace longnose suckers display Bering mitochondrial haplotypes. Further research on widespread species such as pygmy whitefish, burbot, and slimy sculpin may clarify the relationship between the upper Peace fish fauna and northern refugia (i.e., the Bering or Nahanni refugia).