FISHERIES RESEARCH BOARD OF CANADA

BULLETIN 173

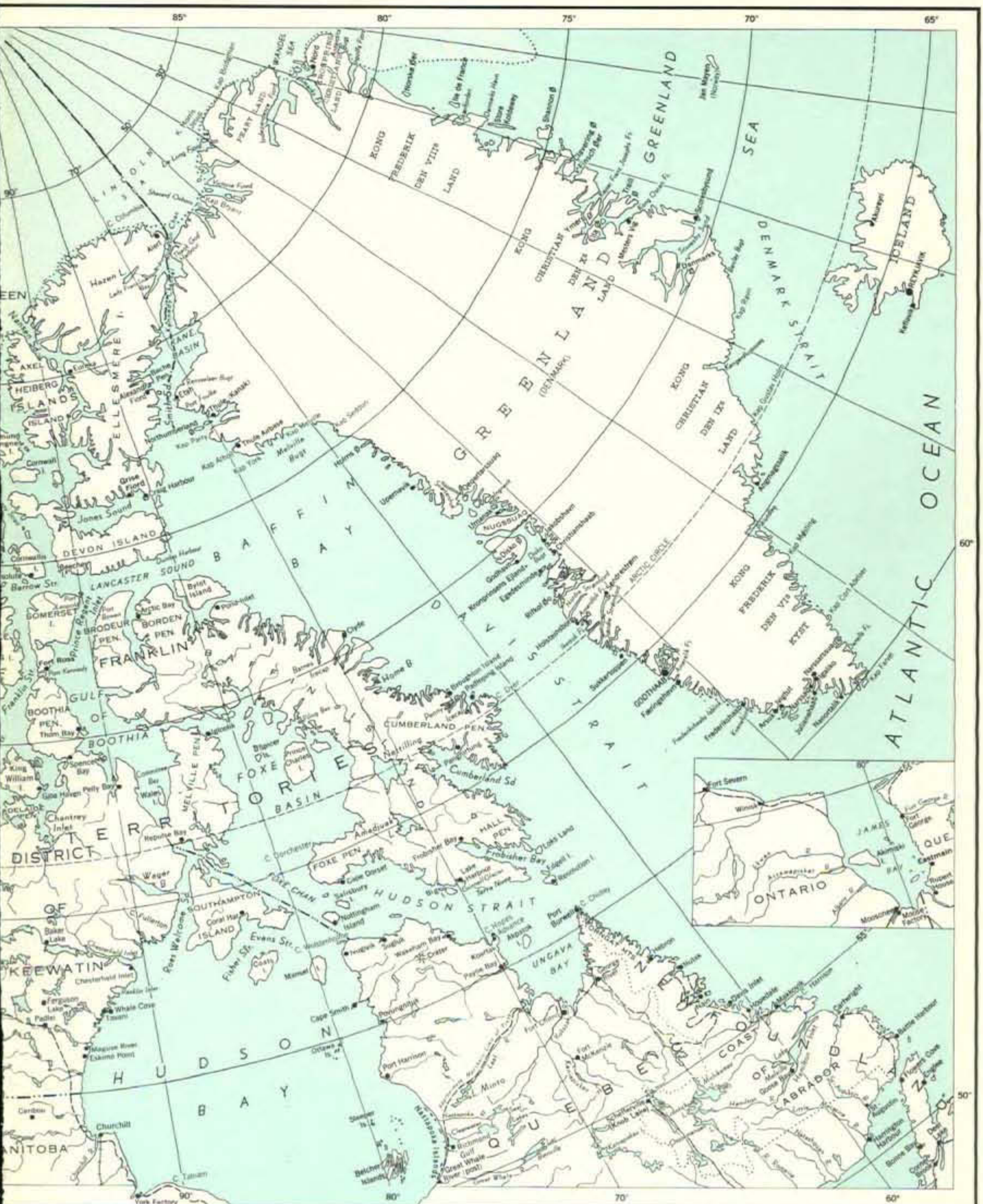
FRESHWATER FISHES OF NORTHWESTERN CANADA AND ALASKA

J. D. McPHAIL AND C. C. LINDSEY

OTTAWA 1970

ALEUTIAN ISLANDS
BERING SEA
Attu Island
Near Islands
Rat Islands
Andreanof Islands
Fox Islands
Dutch Harbor
Unalaska I.
Shumagin Islands
ARCTIC OCEAN
BEAUFORT SEA
CHUKCHI SEA
BERING STRAIT
BERING SEA
U. S. S. R.
BROOKS RANGE
ALASKA
ALASKA RANGE
ALASKA PENINSULA
KENAI PEN.
SEWARD PEN.
GULF OF ALASKA
PACIFIC OCEAN
YUKON TERRITORY
MACKENZIE MTS.
DISTRICT OF MACKENZIE
NORTHWEST
BRITISH COLUMBIA
ALBERTA
SASKATCHEWAN
WHITEHORSE
BANKS ISLAND
VICTORIA ISLAND
DISTRICT
AMUNDSEN GULF
GREAT BEAR L.
GREAT SLAVE L.
Coronation Gulf
MELVILLE ISLAND
VISCOUNT MELVILLE
ISLANDS
Approximate Limit of Permanent Polar Pack Ice
APPROXIMATE SCALE OF MILES
0 100 200 300 400

MCR 2



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FRESHWATER FISHES OF NORTHWESTERN CANADA AND ALASKA

Bulletin 173 OF THE FISHERIES RESEARCH BOARD OF CANADA

Freshwater Fishes of Northwestern Canada and Alaska

J. D. McPhail

Institute of Animal Resource Ecology and Department of Zoology
The University of British Columbia, Vancouver, B.C.

C. C. Lindsey

Department of Zoology
The University of Manitoba, Winnipeg, Man.

FISHERIES RESEARCH BOARD OF CANADA
Ottawa, 1970

Frontispiece opposite: Arctic char, carved from caribou antler by ARNAYUINNAR, of Eskimo Point, N.W.T. Photo: C. C. Lindsey.

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BACKGROUND INFORMATION

INTRODUCTION

The act of publishing a new book sometimes discourages further research, if it creates an impression of completeness or tidiness in the field covered. We hope and expect that the opposite effect will be achieved by this Bulletin. In it we deal with the freshwater fishes in over 2 million square miles of one of the most sparsely populated regions of the globe. The reader will soon be struck by the vastness of the field attempted, and by the scarcity of knowledge. We have tried to bridge some of the gaps by conjecture or by extrapolation from what is known elsewhere. But principally we hope to draw attention to a host of questions waiting to be answered.

The days of exploration, waning on most of the earth, are not yet closed in the north country. New forms of freshwater life may yet be discovered, particularly in the dry unglaciated regions of Alaska, and perhaps in the Canadian Arctic Archipelago. Over the whole of our area, collections are pitifully few except along routes of communication. Fish in the Barren Grounds of Canada are scarcely known; the fresh waters toward Melville and Boothia peninsulas in the northeast have yet to be sampled. Even where specimens have been collected, little is known of the habits of the living animals.

But the great scientific importance of this region does not lie in the discovery of unnamed species therein. It lies in the relative simplicity of the freshwater communities, their relative recency, and their relative freedom from human disturbance. On all these counts, man's urgent need to understand ecological interactions in populated parts of the world can be served by first studying simpler northern communities. There are only about 60 species of freshwater fish in the whole of our region, compared with over 170 species in the much smaller basin of the Great Lakes. The complex effects of competition, predation, or of commercial fishing can be unravelled more easily when only a few species are involved; understanding gained in the north can then be applied in the south. In the north exist many virgin freshwater communities, unaffected by exploitation or pollution. These are the "befores" that must be studied if we are to understand, and control, the "afters" that we have already created wherever man is abundant.

Because of its recent glaciation, this region is also uniquely useful for evolutionary studies. Colossal ice sheets covered most of the area until a few thousand years ago. During the glacial period freshwater animals were confined in a few widely separated refuges around the periphery of the ice. Fish in isolated refuges sometimes diverged enough that their descendents are still distinguishable. Hence the routes can be traced whereby many species moved out into the ice-freed lands in the wake of the retreating ice. Situations can be studied where two slightly different forms met. This Bulletin stresses the phenomena associated with postglacial dispersal, for there is probably no better region on earth for their investigation.

The Bulletin is planned to serve several purposes and several audiences, thereby ensuring that every reader will be dissatisfied with at least some of its sections. Chapters on history and recent geology will provide an introduction for readers unfamiliar with the region. Zoogeographic patterns and dispersal routes are first summarized for the whole region, and then each species is described and discussed individually. The keys, the illustrations, and the sections labelled "Distinguishing Characters" and "Biology" should serve the nonspecialist. The maps contain many previously unpublished locality records, which together with the "Distribution" sections form a summary of present distributional knowledge. The "Description" and "Taxonomic Notes" sections combine old and new information; their zoogeographic interpretation for each species is suggested under "Postglacial Dispersal." The scope of the various sections is described under "Scope of Species Descriptions." We have attempted to include references to relevant literature published up until 1967.

The area covered includes drainages on the North American mainland that are tributaries either to the Bering Sea, to the Arctic Ocean from Bering Strait to Hudson Bay, or to the west side of Hudson Bay south to 60°N. Also included are St. Lawrence Island in the Bering Sea and islands of the western Canadian Arctic Archipelago. Place names can be found on the end sheet maps. All freshwater and anadromous fish species known from this area are illustrated and described. Species that occasionally enter fresh water in the area, or that occupy fresh waters adjacent to the area, are included in the keys. The keys, therefore, cover not only the area described above but also all of Alaska, and waters of Quebec tributary to Hudson Bay.

In preparing this manuscript, intermittently over 11 years, the two authors shared work in the field, in the museum, and in the writing. The order of our names in authorship has been decided after completion by the toss of a coin.

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Many persons in many places have aided in the preparation of this Bulletin, by providing specimens, or information, or assistance in the field. We gratefully acknowledge: W. D. Addison, C. L. Anderson, R. Armstrong, N. Aspinwall, M. V. Atton, D. Ayotte, R. M. Bailey, A. W. Beadell, J. H. Brown, R. L. Burgner, the late W. A. Clemens, D. M. Cohen, B. B. Collette, E. J. Crossman, J. Dowsett, M. J. Dunbar, the late J. R. Dymond, P. J. Ellickson, W. K. Elliott, D. V. Ellis, J. A. Elson, F. H. Fay, H. D. Fisher, W. C. Freihofer, J. H. Gee, G. H. Geen, R. Glover, S. J. Harbo, G. F. Hartman, C. L. Hubbs, J. G. Hunter, J. J. Keleher, S. Y. Koo, L. Johnson, E. D. Lane, P. A. Larkin, J. C. Lyons, E. S. Marvich, D. E. McAllister, J. A. McCabe, P. J. McCart, I. A. McLaren, D. R. Miller, the late R. B. Miller, R. R. Miller, T. Narita, D. W. Narver, J. S. Nelson, T. G. Northcote, D. Paddock, M. J. Paetz, R. R. Parker, B. Paull, A. Peden, S. Pennoyer, Father Poole, E. B. Reed, K. E. Ricker, W. B. Scott, R. Schweitzer, G. D. Taylor, R. S. Taylor, R. Tremblay, E. H. Vernon, R. L. Wallace, G. W. Watson, N. J. Wilimovsky, and I. L. Withler. We are particularly indebted to D. E. McAllister of the National Museums of Canada for his generous criticism of the manuscript.

Between 1957 and 1967 we have received financial or other assistance towards this study from the National Research Council of Canada, the Arctic Institute of North America, the Institute of Fisheries and the H. R. MacMillan Expeditions Fund and the President's Fund of the University of British Columbia, the Department of Zoology of the University of Manitoba, the Arctic Unit (now Arctic Biological Station) of the Fisheries Research Board of Canada, the Fisheries Research Institute of the University of Washington, the Alaska Department of Fish and Game, and the U.S. Fish and Wildlife Service.

Vianney Legendre kindly assisted in selection and coining of French common names of fishes.

While examining museum collections we have received kindness and cooperation from curators of the following institutions: the Royal Ontario Museum, the National Museums of Canada, the United States National Museum, the Museum of Zoology of the University of Michigan, and the Museum of Fishes at Stanford University. We thank the many people, often not individually acknowledged, whose cumulative data stored in these museums are synthesized in this book.

HISTORY OF PUBLICATIONS ON NORTHERN FRESHWATER FISHES

Aboriginal man in the north was sometimes heavily dependent on freshwater or anadromous fishes for food. Some of the ingenious fishing techniques developed by Eskimos and northern Indians are described by Rostlund (1952).

Fishing success was often a matter of life or death to early explorers and fur traders in the north. Preble (1908) wrote "So important are whitefish as an article of diet that the sites of many, perhaps the majority, of the trading posts, as well as the wintering stations of a number of exploring expeditions, places which have become famous in Arctic literature, have been selected with a view to the local abundance of this fish." Entries in the journals of Samuel Hearne, Alexander Mackenzie, Warburton Pike, and Frank Russell describe the parties going hungry because the gillnets were empty. Unfortunately those writers were usually less interested in identifying than in consuming their catch. So also were many of the journal keepers of Hudson's Bay Company. Only common names were recorded, and the actual species encountered usually cannot be determined.

The first scientific account of freshwater fishes from northern Canada was by Forster (1773), who examined a "choice collection of skins of quadrupeds, many fine birds and some fish" collected by servants of the Hudson's Bay Company. Pennant's *Arctic Zoology* (1784) also contained descriptions and brief notes on some North American fishes.

Scientific investigation of the north received a tremendous impetus by the prize of £20,000 offered in 1818 by the British government for discovery of the Northwest Passage. In the flurry of exploration that followed, the dominant scientific figure was

John Richardson. As surgeon and naturalist on the first and second expeditions of John Franklin, Richardson spent one winter at Cumberland House on the Saskatchewan River, two at "Fort Enterprise" (at a site now uninhabited on the Snare River drainage about 150 miles north of Yellowknife), and one at Fort Franklin on the outlet of Great Bear Lake. During the two expeditions (1819–22 and 1825–26) Richardson explored the whole arctic coast east from the Mackenzie delta to Bathurst Inlet. The specimens and experience he and his assistant collected led to publication of the monumental *Fauna Boreali Americana,* in Part 3 of which (1836a) he discussed 140 species of marine and freshwater fish, many of them new to science. Six of the species included in the present bulletin were first described in that work.

Sir John Richardson (knighted in 1846) was not on Franklin's ill-fated third expedition in 1843. During the next dozen years over 40 expeditions were despatched to search for Franklin, including one led by Richardson. Although none found Franklin, his loss contributed enormously through the geographic and scientific information brought back by his searchers. Northern freshwater fishes collected by expeditions led by Parry, Franklin, Ross, Back, Belcher, McLintock, and others are reported in studies by Richardson (1823, 1835, 1836a, b, 1854, 1855), Sabine (1821), Walker (1860), and Gunther (1877a, b).

During the 1840's the Russian naturalist I. G. Vosnesensky collected for 10 years in Russian America (now Alaska) and Kamchatka. His fish collections, however, remained unstudied in the Zoological Museum of the Russian Academy of Sciences until 1904, when P. Yu. Shmidt published on those specimens still remaining.

About the time that British exploration of the Canadian north waned, interest in northern fish was awakening amongst scientists from the United States of America. Robert Kennicott was a likeable and energetic naturalist responsible for the acquisition of important northern collections in the Smithsonian Institution (now the U.S. National Museum). Between 1859 and 1862 he travelled extensively in central British America and portions of Russian America, collecting on the Liard, Mackenzie, Peel, Porcupine, and upper Yukon rivers. Kennicott instilled the Scottish gentlemen employed at various Hudson's Bay Company posts with enthusiasm for the pursuit and preparation of natural history specimens. The Company provided free lodging and transport of specimens; the Smithsonian Institution issued a circular for the benefit of personnel of the Company, indicating the types of information and material needed. Some senior employees became avid collectors, and, for many years after, collections poured into Washington from the north, until those who had been inspired by Kennicott retired from active service. In 1865 Kennicott became Chief of Explorations on the survey for the proposed Overland Telegraph to Russia, and was responsible for biological exploration around Norton Sound on the Bering Sea. He died tragically at Nulato on the Yukon River. His journals contained notes on 22 species of freshwater fishes, indicated only by common name (James, 1942). His successor as Chief of Explorations, W. H. Dall, published in 1871 the first list of freshwater fishes from Alaska; some of the erroneous scientific names Dall used were corrected by Bean (1887).

After the purchase of Alaska from Russia in 1867, the tempo of American research there increased. T. H. Bean, Curator of Fishes at the U.S. National Museum, wrote many important papers on Alaskan freshwater species (Bean, 1879b, 1881b, c, 1882, 1883, 1884, 1885, 1887, 1888b, 1890a, b, 1892) as well as on specimens collected by others in northern Canada (Bean, 1879a, 1881a, 1888a, c). During the 1880's and 1890's the rich Alaskan fisheries stimulated many other researchers, working principally on salmon. Papers of this period on Alaskan freshwater fishes are by Murdoch (1885), Turner (1886), Nelson (1887), Gilbert (1895a), Evermann and Smith (1896), Jordan and Gilbert (1899), Scofield (1899), Stoney (1899), Cantwell (1902), Fowler (1904, 1905), and Evermann (1905). Knowledge was consolidated in Chamberlain's study on Alaskan salmon and trout (1907), Evermann and Goldsborough's compiled *Fishes of Alaska* (1907a), and, on a wider scale, in Jordan and Evermann's 4-volume *Fishes of North and Middle America* (1896–1900).

Exploration of the Canadian north was now pursued by employees of the Canadian government such as Andrew Halkett of the Department of Fisheries (Halkett, 1898, 1913, 1920, 1928), and by many men of the Geological Survey who had broad scientific interests and who collected data on fish (Macoun, 1888; Dawson as reported by Bean, 1888c; Williams, 1922). Various other expeditions, some publicly and some privately financed, brought back specimens. In 1892 an unattached American lady named Elizabeth Taylor made a summer trip by means of the regular conveyances of the Hudson's Bay Company to the lower Mackenzie River and back. Although she was the first woman tourist in this area, no serious disruption is recorded amongst the Company servants, and the fishes she collected were duly reported on by the U.S. National Museum (Gilbert, 1895b), as were the butterflies and other specimens. A more orthodox and much more important survey of the Athabasca–Mackenzie region was undertaken by the U.S. Bureau of Biological Survey in 1901 and 1903–04. The resulting publication by Preble (1908), in the *North American Fauna* series, remains today an authoritative reference on history and geography as well as on biology. Using data from Preble and others, Evermann and Goldsborough (1907b) produced at this time a checklist of the freshwater fishes of Canada.

The Stefansson–Anderson expedition of 1908–12, supported by the American Museum of Natural History and the Geological Survey of Canada, collected along the arctic coasts of Canada and Alaska; information on fishes was recorded by Anderson (1913). On the Canadian Arctic Expedition of 1913–18 Frits Johansen collected fishes in Alaska and the western Canadian arctic; these were reported on much later by Walters (1953). Johansen's extensive field notes and coloured drawings were not seen by Walters, but are evidently still extant in the U.S. National Museum (Dymond, 1964), and a voluminous manuscript intended for publication by Johansen exists in the files of the ichthyological section of the National Museums of Canada.

Specimens collected by Francis Harper on several expeditions to northern Canada were discussed by Harper and Nichols (1919), Kendall (1924), Fowler (1948), and Harper (1948, 1961). Reference was made to freshwater fishes of particular areas by Kendall (1917, 1921, Bristol Bay drainages), Kemp (1928) and Dymond (1940, lower Mackenzie River), Soper (1928, 1934, Baffin Island), Critchell-Bullock (1931) and Clarke (1940, Thelon River), Henn (1932) and Manning (1942, Southhampton Island), Pfaff (1937, Keewatin and vicinity), and Hubbs and Schultz (1941, Alaska). A government-sponsored search for commercial fisheries in Hudson Bay produced several publications that included reference to freshwater forms (Cox, 1920; Walker, 1931; Dymond, 1933; Vladykov, 1933).

During World War II (1939–45) the Fisheries Research Board of Canada launched for strategic reasons a survey of the fishery potential in northern fresh waters. Government and university scientists collected intensively for the first time in the larger northern lakes of Canada, including Teslin, Athabasca, Great Slave, and Great Bear lakes. Southern Yukon Territory and the mainstem of the Mackenzie River were included in the survey. A joint Fisheries Research Board Bulletin and many separate papers followed (Clemens et al., 1945; Kennedy, 1949, 1953; Miller, 1946, 1947; Miller and Kennedy, 1948a, b; Rawson, 1947a, b, 1951; Wynne-Edwards, 1947a, b, 1952).

Fishery research in northern Canada, stimulated by the wartime survey, has not abated since. An Arctic Station of the Fisheries Research Board of Canada in Montreal was established to promote far northern investigations. In 1959 it carried out a large-scale air-borne survey of the Barren Grounds covering major parts of the Mackenzie and Keewatin districts of the Northwest Territories. Staff members of the Royal Ontario Museum and of several Canadian universities participated. Parts of the Arctic Archipelago were surveyed in 1962. Much of the material collected in these surveys has been incorporated into the present Bulletin. We have also incorporated data collected by ourselves on trips between 1956 and 1965, ranging from northern Alberta to Victoria Island and from Bristol Bay to St. Lawrence Island in the Bering Sea.

Faunal studies in the southern portion of our area include Hinks (1957, Manitoba), Rawson (1947c, 1959, Saskatchewan), MacDonald (1951, Alberta), Carl et al. (1959) and Lindsey (1956, 1957, British Columbia). Compilations of freshwater fishes of all Canada were prepared by Dymond (1947), Slastenenko (1958), and Scott (1958).

Alaska does not support as large a fishery on purely freshwater species as does northern Canada. But the Bering Sea drainages of Alaska provide spawning grounds for enormous numbers of Pacific salmon. Hence research on fresh waters of Alaska, which has been extensive, has concentrated mainly on matters affecting the freshwater stages of the various salmon species. There is voluminous literature, much but not all of it oriented towards salmon management, in publications of the U.S. state and federal agencies. These include the Bureau of Commercial Fisheries, and the Bureau of Sports Fish Management (both of the U.S. Fish and Wildlife Service), the Alaska Department of Fish and Game, the Fisheries Research Institute at the University of Washington, and the International North Pacific Fisheries Commission. Pertinent references in these or other publications include Dufresne (1946), Wohlschlag (1953, 1954), Cohen (1954), Wilimovsky (1954, 1958), and Greenbank (1954). A comprehensive treatment of *Fishes of Western Arctic America and Eastern Arctic Siberia* was published by Walters in 1955.

Particular groups of northern fishes have been treated by Dymond and Vladykov (1933, salmonids), Dymond (1943, northwestern coregonids), Norden (1961, salmonids, especially grayling), McAllister and Lindsey (1961, *Cottus*), Vladykov (1962, Pacific salmons), and McAllister (1963, osmerids). Many other papers dealing with one or a few northern species are cited throughout this Bulletin.

For identification of freshwater fishes outside the range covered by this Bulletin, the most useful reference is *Fishes of the Great Lakes Region* by Hubbs and Lagler (1964). Others are by Backus (1957, Labrador), Legendre (1954, Quebec), Hinks (1957, Manitoba), and Carl et al. (1959, British Columbia). Moore (1957) provides simple keys to all freshwater species in the United States. Jordan and Evermann's *Fishes of North and Middle America* (1896–1900) though old is still useful in giving detailed taxonomic descriptions, and has been reprinted. Marine fishes are discussed in Leim and Scott (1966, Atlantic), McAllister (1960, 1962, arctic Canada), Walters (1955, western arctic America and eastern arctic Siberia), Wilimovsky (1958, 1964, Alaska and Aleutian Islands), Clemens and Wilby (1961, Pacific). Berg's monumental *Freshwater Fishes of the U.S.S.R.* (1948–49) is available in English translation.

Discussions of postglacial dispersal of northern North American freshwater fishes include Greene (1935), Radforth (1944), Wynne-Edwards (1952), Walters (1955), Lindsey (1956), Underhill (1957), and Metcalfe (1966), in addition to papers dealing with particular species, which are cited later.

Fuller histories of ichthyology than have been given here are provided by Preble (1908, Mackenzie region), Dymond (1964, Canada), and Myers (1964) and Hubbs (1964, United States). An annotated bibliography on freshwater fishes in the region covered by this Bulletin has been prepared by McPhail (1960).

OUTLINE OF GEOLOGICAL HISTORY

Enough is known of events during the Pleistocene glaciation to reveal some correlations between geological evidence and present fish distributions. Our knowledge is still fragmentary, but information is accumulating rapidly. Soon it should be possible to examine the causes behind northern zoogeographic patterns more thoroughly than we have done here.

The Pleistocene era occurred during roughly the last 1 million years, following a very much longer warm period. During this era there were probably four principal cold periods: the oldest (called the Nebraskan in North America) occurred about 1 million years ago, the second (the Kansan) about 700,000 years ago, and the third (the Illinoian) about 300,000 years ago. The last glacial period, called the Wisconsin, is currently believed to have started about 50,000 years ago and ended about 10,000 years ago. Between each glacial period the climate was equivalent to or somewhat warmer than present conditions. Each advancing ice sheet tended to obliterate traces of its predecessor, so we know little of glacial events previous to the Wisconsin. However, the second-last or Illinoian glacial period was more severe than the others; the southern limit reached by Illinoian ice has therefore not been over-ridden by the last (Wisconsin) ice. It is often difficult to distinguish the age of glacial evidence such as scratches on rock. Hence an area may bear unmistakable evidence of having been glaciated *at some time,* yet we are unsure whether parts of the area may have been ice-covered during the Illinoian but ice-free during the less severe Wisconsin period. The possible existence of ice-free refuges during the Wisconsin is clearly important to zoogeographic understanding. Intensive study is required on a number of such suspected pockets.

The onset of each glaciation involved a climatic shift, perhaps rather slight, that was triggered by causes not yet understood. Growth or recession of an ice mass can result from any upset in the balance between the amount of snow accumulating through precipitation and the amount disappearing through melting and evaporation. The Wisconsin period probably started by gradual buildup of local ice masses over high ground along the western mountains and also in Labrador, Baffin Island, and Keewatin. As ice accumulated, local masses fused to form two principal ice sheets, the Cordilleran in the west and the Laurentide in the east (Fig. 2). These increased to a thickness of several thousands of feet, and began to flow out from their centres of accumulation, eventually pushing ice tongues far to the south. The Laurentide sheet oozed westward across central Canada and met the Cordilleran sheet along the eastern foothills of the Rocky Mountains, so that almost all of Canada and a strip of the northern United States was ice-covered (Fig. 2).

Although details are obscure, there is evidence from buried valleys that the drainage patterns of North America prior to glaciation differed somewhat from those of the present. Many tributaries of the upper Missouri River in Wyoming, Montana, and the Dakotas now flow northeast before turning sharply at their junction with the present main river (Fig. 2). Borings and subsurface geophysical exploration indicate that these tributaries once formed the headwaters of a large drainage system continuing northeast towards what is now Hudson Bay (Fig. 1). Whether this pattern existed during any of the interglacial intervals as well as in pre-Pleistocene times is unknown.

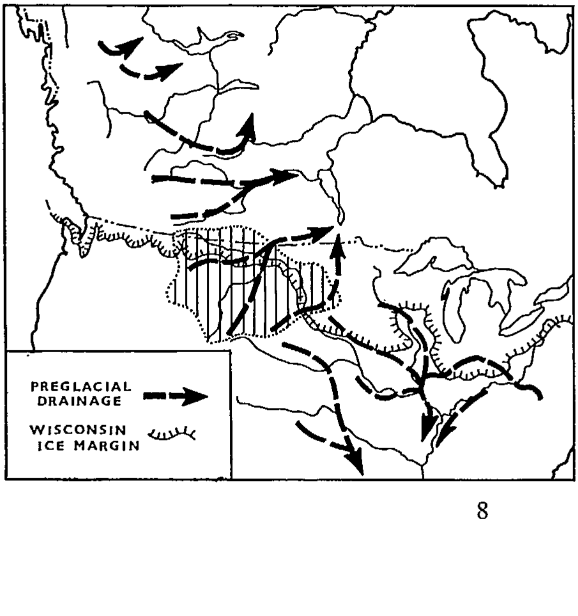


Fig. 1. Drainage systems before Pleistocene glaciation. Hatched area now tributary to Missouri River was formerly tributary to Hudson Bay basin (after McCrossen and Glaister, 1964; Metcalfe, 1966).

With the advance of ice from the northeast, outlets towards Hudson Bay were blocked. Water then escaped to the east and south towards the Mississippi River, flowing along the ice margin at or close to the present course of the Missouri River. A channel was carved so deeply that this drainage pattern persisted even after ice withdrawal. The Missouri River now flows at right angles to much of the regional slope of the land it traverses. That this kind of event happened more than once is indicated by an abandoned channel system parallel to the Missouri trench but southwest of it, with a length of more than 150 miles (Flint, 1957).

Other differences between preglacial and present drainages (Fig. 1) are described by Metcalfe (1966). A preglacial Great Plains River flowed from north to south across the present state of Kansas. East of this lay the ancestral Mississippi, with a long eastern tributary, the Teays River, whose wide deep trench has since been filled by glacial debris.

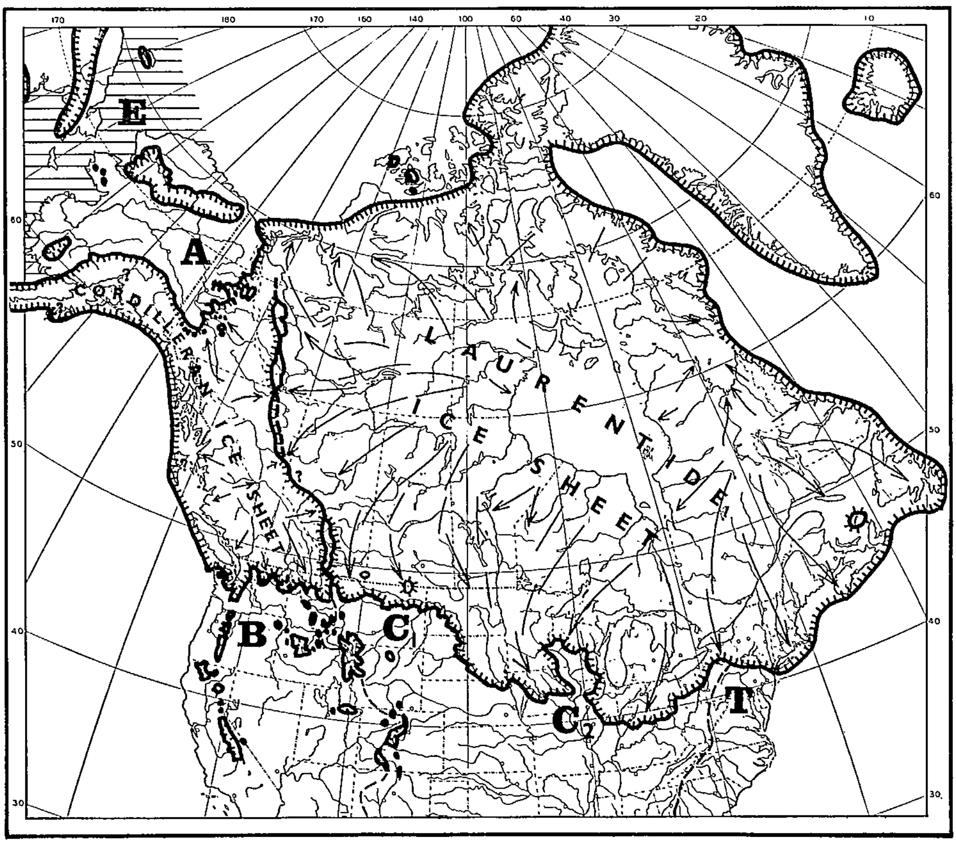


Fig. 2. Maximum extent of glaciation during Wisconsin period (indicated by hachures). Fine arrows suggest directions of ice advance. Refuges for freshwater fishes indicated by letters: A = Alaska, B = Pacific, C_1 = Missouri River, C_2 = Upper Mississippi River, E = Exposed Bering land bridge, T = Atlantic. (After Wilson, 1958; Flint, 1945; Hopkins, 1959; Sachs and Strelkov, 1961.) Glaciation limits for western Brooks Range may be Illinoian, not Wisconsin.

The ancestral Hudson Bay drainage, which included much of the area now drained by the Missouri, may have existed for a very long time before the first Pleistocene glaciation. It probably developed a fish fauna somewhat distinct from that of the south-draining Mississippi–Teays and Great Plains rivers. As ice advanced south, organisms in the Hudson Bay drainage would have been forced south until they occupied only that southwestern portion of the drainage that was not occluded by ice (in Fig. 1, the hatched area lying south of the glacial margin). During maximum glaciation some mixing of Hudson Bay and Mississippi or Great Plains stocks must have occurred, both by southward escape of Hudson Bay components down the new southeastern outlet, and by invasion of the former Hudson Bay tributaries by southeastern forms. Complete mixing was probably prevented by the retention of pockets of pure Hudson Bay forms or pure southern forms above impassable waterfalls in tributaries within their respective areas. Ecological adaptations may also have restrained the invasion of northern forms into southern territory and vice versa. Hence, when the ice retreated to the north a pocket of partially distinctive forms within the upper Missouri River system was the source from which central Canada was repopulated. The same process probably occurred with each successive advance and retreat of glaciation. Today we find some species whose regional variation may reflect partial but not complete mixing of these different stocks. In some species such variation does not exist (or has not been detected); these may have intermingled completely, or may never have diverged. At least two distinctive species (the flathead chub, *Platygobio gracilis,* and the goldeye, *Hiodon alosoides*) have modern ranges including the area originally encompassed by the arctic and the Hudson Bay drainage systems, but even now excluding the Great Lakes; these fish perhaps first evolved in the ancestral Hudson Bay drainage.

Patterns of variation in more southerly areas of the Great Plains have been similarly discussed by Metcalfe (1966). All attempts to relate present variation to preglacial divergence are necessarily conjectural. Experimental studies are needed to determine whether variation is hereditary or is due to the direct effect of the environment on the developing young. If it is the former, studies on physiological tolerances might confirm or deny that present differences suggest adaptation to conditions in separate ancient drainages.

Turning to events after the maximum Wisconsin glaciation, we have rather more information from which to speculate. During the Wisconsin maximum, freshwater fishes must have persisted in a number of refuges around the ice margin. A large part of the Yukon River basin (A in Fig. 2) escaped glaciation. The high mountain ranges surrounding the Gulf of Alaska now catch much of the moisture carried by Pacific air, and produce a "rain shadow" inland in the Yukon River valley. The valley was probably dry during the Wisconsin period (as it is now) preventing the buildup of extensive snow fields despite low temperatures.

The locking up of so much water in the ice sheets of the Wisconsin period led to a world-wide drop in sea level. A strip of land over 1000 miles from north to south emerged connecting Alaska and Siberia. This Bering land bridge (E in Fig. 2) had only a tundra vegetation (Hopkins, 1959), but carried a network of rivers and shallow lakes through which freshwater fishes could pass. St. Lawrence Island in the Bering Sea is a remnant of the land bridge.

Some western islands of the Canadian Arctic Archipelago, notably Banks, Prince Patrick, and Melville, partially escaped glaciation (Fig. 2). Also portions of the Mackenzie Mountains projected as uncovered "nunataks" above the ice sheets. South of the principal Bering refuge other areas may have escaped complete glaciation, including parts of Kodiak Island, the Cook Inlet area, the Copper River basin, perhaps Queen Charlotte Islands (Heusser, 1960; Karlstrom, 1961), and offshore areas exposed at that time by the sea-level drop (Klein, 1965).

South of the ice and west of the Rocky Mountains lay a refuge for many freshwater species (B in Fig. 2). The Pacific slope of North America was probably isolated from the rest of the continent for a long time preceding the Pleistocene, and developed many distinctive genera and species of freshwater fishes. Most have apparently shifted north and south during successive Pleistocene glaciations without an opportunity to cross the Continental Divide eastward; it is only in recent times that several West Coast species have crossed by entering the upper Peace River from the Fraser (Lindsey, 1956).

The principal source from which freshwater fishes repopulated British Columbia after glacial retreat was the Columbia River basin, which probably included more lakes during the Wisconsin period than it does now. The Pacific coast and more easterly refuges probably presented a tundra environment near the edge of glaciation (as did the whole of the Bering refuge) but this gave way to a more equitable boreal climate within a few miles of the ice margin (Dorf, 1959). Larger and more diverse faunas survived in these southern refuges than in the Bering refuge.

The third major refuge for freshwater fishes lay south of the Wisconsin ice sheet between the Appalachians and the Rocky Mountains. Reasons why the region of the upper Missouri (C_1 in Fig. 2) contained a fauna somewhat distinctive from that of the upper Mississippi (C_2) and Ohio rivers have already been outlined. Moreover, during the early Wisconsin the Missouri River was twice diverted by the southward protruding James icelobe and drained south across Nebraska into the Platte River (Simpson, 1960). This resulted in partial isolation of the upper Missouri and upper Mississippi rivers. The Missouri was not diverted during the Mankato or later ice advances within the Wisconsin period, and many species were probably continuously distributed from the upper Missouri system to the Ohio valley at this time.

Some freshwater fishes probably survived the Wisconsin east of the Appalachians on the Atlantic coast (T in Fig. 2). We do not know of any species originating exclusively from this refuge that has invaded our area.

In summary, during the maximum extent of the last glaciation those freshwater fishes that later invaded our area were effectively isolated in three principal pockets: the Bering refuge, the Pacific refuge, and the northern tributaries of the Gulf of Mexico drainage.

As the Wisconsin ice sheets began to retreat, large areas were exposed into which fishes from various refuges were able to spread. There were two main avenues by which fishes entered the freshly deglaciated regions: coastal dispersal by way of the sea, and inland dispersal through drainage changes. The latter route was particularly important in north-central North America where a complicated series of proglacial lakes was formed by the hesitant retreat of the ice.

Dispersal through both the inland and coastal routes was controlled by the detailed pattern of deglaciation. Ice did not retreat uniformly to the north; in coastal regions the ice apparently withdrew inland fairly rapidly, but in other regions (notably the Great Lakes area) the retreat was marked by a series of advances and withdrawals. Deglaciation is better documented in the Great Lakes area than elsewhere (Flint, 1957; Hough, 1958). The Wisconsin Laurentide ice sheet was at its maximum in the Great Lakes region about 18,000 BP (Before Present). By 13,000 BP parts of the basins of lakes Michigan, Huron, Erie, and Ontario were exposed. Large glacial lakes formed in these basins, and drained south into the Mississippi system, or east into the Susquehanna River, or by both routes. This period culminated in a slight readvance, the Mankato (or Port Huron?) maximum about 12,500 BP. During the next 1000 years (Two Creeks interval) the ice retreated farther north, and glacial Lake Keweenaw formed in the exposed portion of the Lake Superior basin.

The Two Creeks interval was followed by a major readvance, the Valders maximum, about 10,600 BP. The Lake Superior and Lake Ontario basins were considerably reduced. Drainage was mainly south into the Mississippi system.

After the Valders maximum the ice retreated rapidly, and by about 8000 BP most of the Great Lakes area was ice-free. At this time drainage was south into the Mississippi system and east into the Hudson River. When the ice retreated beyond the Hudson Bay drainage divide, Lake Barlow-Ojibway was formed (Fig. 3); it first drained to the southeast into the St. Lawrence system, and was probably connected to Lake Agassiz about 8000 BP (Elson, 1967). A minor readvance may have later covered part of the Lake Barlow-Ojibway basin. Differential uplift in the northern part of the Great Lakes region resulted in the Nipissing Great Lakes about 4000 BP. At this time drainage was south into the Mississippi system and northeast into the St. Lawrence River. The present drainage was established with the closure of the last outlet to the Mississippi system about 2000 BP.

Deglaciation on the Atlantic coast was earlier and more rapid than in the Great Lakes region. Initial ice retreat in the Long Island Sound area began about 30,000 BP (Newman and Fairbridge, 1960). By the Mankato maximum the ice had retreated to the Boston area (Ogden, 1959), and most of Nova Scotia was ice-free by 10,000 BP (Hickox, 1960; Livingstone and Livingstone, 1958). Ives (1959, 1960) indicates that the coastal areas of Labrador were also ice-free by about 10,000 BP, but a residual ice mass remained in the Schefferville area until about 6000 BP.

On the Atlantic coast deglaciation was followed by marine submergence, and the sea flooded the St. Lawrence lowlands to form the Champlain Sea. The Champlain Sea was perhaps contemporary with the Two Creeks interval (Terasmae, 1959). La Rocque (1949) suggests that a marine connection existed for a time between James Bay and the Champlain Sea across Lake St. John.

On the Great Plains the southern edge of the Laurentide ice sheet extended in a northwesterly direction from Illinois to the Rocky Mountains (Fig. 2). At the

Wisconsin maximum drainage was south into the Missouri and Mississippi rivers. With the ice retreat after the Mankato maximum, Lake Agassiz I was formed in southern Manitoba and North Dakota about 12,000 BP. Lake Agassiz I first drained south through the Warren River into the Mississippi system; later it emptied east into the Lake Superior basin, and its level was lowered (Elson, 1967).

An ice readvance formed Lake Agassiz II in the same area. Lake Agassiz II first drained south by the Warren River into the Mississippi system. As ice then retreated northward, a northwesterly drainage may also have been established about 9500 BP (Elson, 1967). Outlets then opened into the Lake Superior basin again. About 8000 BP Lake Agassiz emptied east into Lake Barlow-Ojibway (Fig. 3), and finally disappeared as outlets were established to Hudson Bay.

Ice retreat on the western Great Plains was in a northeasterly direction (Gravenor and Bayrock, 1961). Southern Alberta and southwestern Saskatchewan became ice-free relatively early in deglaciation. In fact the Laurentide and Cordilleran ice

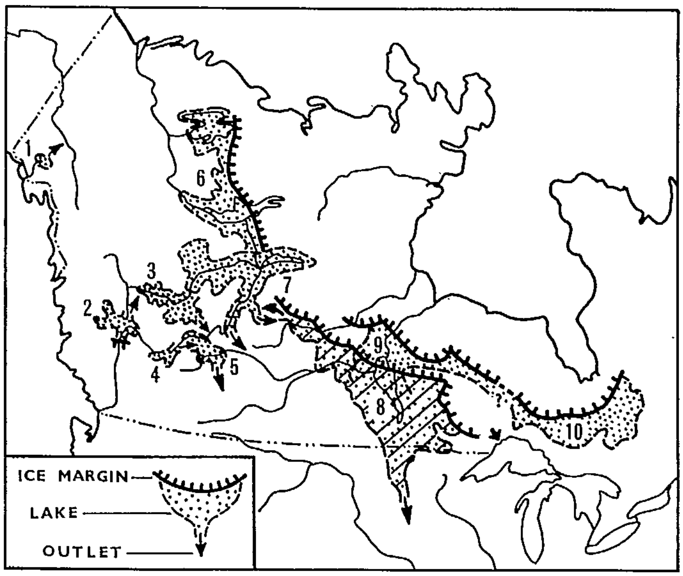


Fig. 3. Some extinct postglacial lakes, selected to illustrate drainage patterns that crossed present drainage boundaries during glacial retreat. The lakes shown did not exist all at the same time. 1. Glacial Dezadeash Lake: present Alsek River basin drained to Yukon River (Wilson, 1958). 2. Prince George basin: present Fraser River basin drained to Peace River (Armstrong and Tipper, 1948). 3. Lake Peace: present Mackenzie River basin drained southeast (Taylor, 1960). 4. Miette Lake: present Fraser River basin drained east over Continental Divide (Taylor, 1960). 5. Lake Edmonton: present Athabasca River (Mackenzie basin) and North Saskatchewan River (Hudson Bay basin) joined, drained south (Taylor, 1960). 6. Glacial Lake McConnell, united Great Bear, Great Slave, and Athabasca lakes (Craig, 1965). 7. Lake Tyrrell: present Mackenzie River basin drained southeast (Taylor, 1960). 8. Lake Agassiz, Campbell phase: present Nelson River (Hudson Bay basin) drained sometimes to Mississippi River, sometimes to northwest (Elson, 1967). Outlets opened later to Lake Superior. 9. Lake Agassiz, Gimli phase: perhaps drained east to Lake Barlow-Ojibway (Elson, 1967). 10. Lake Barlow-Ojibway; present James Bay basin (Wilson, 1958).

sheets never completely met in some areas of western Alberta; isolated and perhaps shifting refuges may have persisted along the east slope of the Canadian Rocky Mountains throughout Wisconsin glaciation. The numerous glacial lakes in southern Alberta were relatively small and short lived. Drainage was south into the Missouri River, and later east into Lake Agassiz.

The regional slope north of Edmonton is to the northeast. When the ice retreated in this area a series of large proglacial lakes was formed; the most important were lakes Edmonton, Peace, and Tyrrell (Taylor, 1960) (Fig. 3). These lakes drained to the southeast, perhaps into Lake Agassiz. Later in deglaciation large glacial Lake McConnell was formed in the Great Slave–Great Bear Basin, which drained south into Lake Agassiz until isostatic readjustment established the present northern drainage.

Along the arctic coast the ice retreated in a southeasterly direction (Craig and Fyles, 1960; Craig, 1960). The arctic coast was ice-free to Coronation Gulf by 10,000 BP (Craig, 1961), and to the Gulf of Boothia by 8000 BP (Craig, 1961). After deglaciation much of the arctic coast of Canada and land surrounding Hudson Bay was submerged beneath the sea.

In the final stages of deglaciation the Laurentide ice sheet split into two separate ice masses and withdrew into Keewatin and Labrador. The division of the ice sheet was caused by the entry of the sea into Hudson Bay. Lee (1960) dates the maximum postglacial submergence of lowlands bordering Hudson Bay at 7000–8000 BP. The sea must have penetrated through Hudson Strait into Foxe Basin and Hudson Bay somewhat earlier. The residual ice masses in Keewatin and Labrador disappeared about 6000 BP. Since then the extensive Hudson Bay lowlands and parts of the arctic coast and islands have risen above sea level.

Little is known about the deglaciation of the Cordilleran ice sheet. Apparently most of the coastal area became ice-free relatively early. Crandell et al. (1958) indicate that the ice retreated from the Seattle area before 14,000 BP, and Armstrong (1956) notes a readvance in the Fraser Valley about 11,000 BP. Some coastal areas as far north as Juneau were ice-free by 10,000 BP (Olson and Broecker, 1959), and glaciated parts of the Kenai Peninsula by 9600 BP (Broecker et al., 1956). The northern Pacific coast is still not completely ice-free, but dispersal along the coast was probably possible by about 9000 BP.

Deglaciation in British Columbia produced many temporary shifts in drainage patterns (Fig. 3). At one time during ice retreat the Thompson River basin of the present Fraser River system was tributary to the Columbia River (Mathews, 1944); at another the northern Fraser system was tributary to the Peace River (Armstrong and Tipper, 1948); Miette Lake once covered the present Yellowhead Lake in the uppermost Fraser River and drained eastward across the present Continental Divide (Taylor, 1960).

Regarding the distribution of freshwater fishes, the two most important points that emerge from our present sketchy knowledge of deglaciation are the early retreat of ice from coastal regions (allowing the rapid dispersal of salt tolerant forms), and the rapid northeasterly retreat of ice from the Great Plains (allowing Missouri forms to enter northern Canada before Mississippi forms had access to the area).

ZOOGEOGRAPHIC PATTERNS

There are about 60 species of freshwater fishes native to our area. Of these, 11 entered our area only from the Pacific refuge, 10 survived glaciation in the Bering refuge, and 18 entered from the Mississippi refuge. The remaining 21 species survived glaciation in more than one North American refuge. The following sections will deal with each of these groups in detail. Subspecific names, and problems arising from the fact that some "species" are probably in reality complexes of species, are omitted in this section but are discussed later under the "Taxonomic Notes" for each species.

(A) Fishes that Entered our Area from the Bering Refuge only

The Bering refuge included the unglaciated regions of Alaska, the Yukon Territory, St. Lawrence Island, and adjacent parts of Siberia (all of which were linked during the Wisconsin by the Bering land bridge already described), and possibly parts of Kodiak Island, the Cook Inlet area, the Copper River basin, and Queen Charlotte Islands. Walters (1955) treats the arctic slope of Alaska and the Yukon Valley as separate refuges, but during the Wisconsin these areas were probably less isolated from one another, due to the fall in sea level, than they are today, and it seems unlikely that they operated as separate refuges except for the anadromous ciscoes, *Coregonus autumnalis* and *C. laurettae*. Kodiak Island may have functioned as a separate refuge for the Arctic char (*Salvelinus alpinus*). Probably plants and mammals and possibly fish survived glaciation in some other of these places, or in areas now offshore but then exposed (Klein, 1965). The fresh waters on the Bering land bridge contained fish; St. Lawrence Island, an unsubmerged remnant that was once the ridgepole of the land bridge, still harbours three freshwater species as relicts of the land-bridge fauna (*Thymallus arcticus, Dallia pectoralis,* and *Cottus cognatus*). No freshwater fishes are known to have survived in the unglaciated highland areas of the Mackenzie Mountains suggested as plant refuges by Heusser (1960), nor in the unglaciated areas of the Arctic Archipelago (which included parts of Banks, Prince Patrick, and Melville Islands), but these areas are still poorly explored. Portions of the Peel River (now tributary to the Mackenzie River delta) were unglaciated (Fig. 2) and probably harboured some fish.

For the following 10 species the Bering area was the only North American refuge during glaciation: *Lampetra japonica* (unless *L. lamottei* is conspecific), *Stenodus leucichthys, Coregonus nelsoni* (if it is a valid species), *Coregonus pidschian, Coregonus sardinella, Coregonus nasus, Coregonus autumnalis, Coregonus laurettae, Hypomesus olidus,* and *Dallia pectoralis.*

Six of these species (*L. japonica, S. leucichthys, C. sardinella, C. autumnalis, C. laurettae,* and *H. olidus*) commonly occur in the sea, and their distribution in northern North America is mainly due to coastal dispersal. *Lampetra japonica, C. laurettae,* and *H. olidus* dispersed in two directions from the Bering refuge: south into the Gulf of Alaska region, and east along the arctic coast. *Stenodus leucichthys, C. sardinella,* and *C. autumnalis* appear to have dispersed only to the east along the arctic coast. Both *L. japonica* and *S. leucichthys* have spread up the Mackenzie system as far as Great Slave Lake whereas *H. olidus* has reached only to Great Bear Lake. *Coregonus autumnalis* and *C. sardinella* are anadromous in the Beaufort Sea area but apparently neither species ascends the Mackenzie River above Camsell Bend.

Two other Bering species (*C. nasus* and *C. pidschian*) are commonly taken in brackish water, and apparently have dispersed through the sea. *Coregonus nasus* has spread east along the arctic coast as far as Perry River and up the Mackenzie River to Camsell Bend. *Coregonus pidschian* has apparently dispersed in two directions: east along the arctic coast to the Mackenzie Delta, and south to the Alsek system (Lindsey, 1963a, b). The eastern limit was probably attained in part by coastal dispersal, whereas the southern limit (Alsek system) was probably attained through inland drainage connections between that system and the Yukon system. (That the Alsek, a Pacific drainage, has received fish by headwater capture from the Yukon River is further indicated by the presence of *Thymallus arcticus* and *Prosopium cylindraceum.* Glacial Dezadeash Lake at the headwaters of the present Alsek River at one time drained north to the Yukon River (Fig. 3).)

Of all the Bering species only the Alaska blackfish (*Dallia pectoralis*) is completely intolerant of sea water. *Dallia* cannot disperse through the sea and as a result has probably not expanded its range postglacially. The only natural extension of the range of *Dallia* into a glaciated area is its penetration into the Chignik River on the south side of the Alaska Peninsula.

The taxonomic status of the remaining Bering species, *Coregonus nelsoni,* is confused. If it is a valid species it apparently has not greatly expanded its range postglacially.

(B) Fishes that Entered our Area from the Pacific Refuge only

The Pacific refuge included the Pacific watershed south of the Cordilleran ice sheet, and perhaps part of the Great Basin (Fig. 2). Most of the fishes in this category probably survived in the Columbia River system. They are: *Entosphenus tridentatus, Prosopium williamsoni, Salmo gairdneri, Spirinchus thaleichthys, Thaleichthys pacificus, Richardsonius balteatus, Ptychocheilus oregonensis, Mylocheilus caurinus, Catostomus macrocheilus, Cottus asper,* and *Cottus aleuticus.*

Seven of these species can tolerate salt water for at least short periods of time, and the distributions of four (*E. tridentatus, S. thaleichthys, T. pacificus,* and *C. aleuticus*) are restricted in our area to coastal regions. They apparently reached our area by northward dispersal along the coast.

Two of the other species that can enter salt water (*S. gairdneri* and *C. asper*) are also found mainly in coastal regions in our area, but in addition they have restricted distributions in the upper Peace River (*C. asper* and *S. gairdneri*) and the upper Athabasca River (*S. gairdneri*). These species have apparently entered our area both by inland and coastal dispersal routes.

The last of the seven species that can enter the sea is the peamouth (*M. caurinus*). This species is less tolerant of sea water than the others, as is reflected in its more limited northern distribution. In our area the peamouth is restricted to the upper Peace and Athabasca rivers, which it could have entered only by inland dispersal.

Two of the anadromous species, *E. tridentatus* and *S. gairdneri*, also occur on the Asian shore, but dispersal into our area has probably been from the Pacific refuge in North America.

The remaining four Pacific species are intolerant of sea water. Of these the northern distributions of three (*C. macrocheilus, R. balteatus*, and *P. oregonensis*) are restricted to the upper Peace system. The other (*P. williamsoni*) is more widespread in the north and is found in the Athabasca, Peace, and Liard rivers. The northern distributions of all of these species must have been attained solely through inland dispersal routes.

(C) Fishes that Entered our Area from the Mississippi Refuge only

The Mississippi refuge included the unglaciated portions of the upper Missouri, the upper Mississippi, and the Ohio River valleys (Fig. 2). The possibility of a distinctive fish fauna remaining from preglacial isolation of an ancestral Hudson Bay drainage and also the likelihood that the upper Missouri and upper Mississippi function as separate refuges for some species have been described under "Outline of Geological History."

Eighteen species entered our area from the Mississippi refuge. They are: *Hiodon alosoides, Coregonus clupeaformis, Coregonus artedii, Semotilus margarita, Platygobio gracilis, Pfrille neogaea, Chrosomus eos, Notropis atherinoides, Notropis hudsonius, Hybognathus hankinsoni, Pimephales promelas, Catostomus commersoni, Percopsis omiscomaycus, Culaea inconstans, Cottus ricei, Perca fluviatilis, Stizostedion vitreum*, and *Etheostoma exile*.

The present distribution of nine species (*S. margarita, P. neogaea, C. eos, N. atherinoides, H. hankinsoni, P. promelas, C. commersoni, C. inconstans*, and *E. exile*) suggests that they were widespread in the Mississippi refuge during glaciation. All of these species are present both in the Missouri and upper Mississippi systems, and probably spread north into our area from both regions. However, because the pattern of deglaciation on the Great Plains was in a northeasterly direction they probably first entered our area from the upper Missouri system.

The northern distributions of all but one of the species (*C. commersoni*) are restricted to the Mackenzie system. The white sucker is present both in the Mackenzie system and in the upper Dubawnt River, and probably entered the Dubawnt from the Mackenzie. The presence of the brassy minnow (*H. hankinsoni*) in the upper Peace and Fraser systems is probably due to dispersal from the Missouri system. The brassy minnow probably spread north from the upper Missouri into the Saskatchewan system and from there into the Peace River. There were numerous postglacial drainage connections between these systems, and although *H. hankinsoni* is not recorded from the Saskatchewan or Mackenzie systems in Alberta it may yet be found there. Possible mode of entry into the Fraser is discussed under notes on "Postglacial Dispersal" for the species.

Two Mississippi species (*H. alosoides* and *P. gracilis*) apparently dispersed north only from the Missouri system. The goldeye is widespread in the Missouri and the lower Mississippi, but is absent from the Great Lakes and upper Mississippi. The presence of *H. alosoides* in Sandy Lake and drainages entering southeastern James Bay suggests that dispersal occurred northward through the final stages of glacial Lake Agassiz, east to Lake Barlow-Ojibway, and northwest through a series of glacial lakes to the Mackenzie system. Possible reasons for absence of goldeyes from the Great Lakes are discussed under notes on "Postglacial Dispersal" for the species.

The flathead chub (*Platygobio gracilis*) is abundant in the upper Missouri but is absent from the Upper Mississippi and the Great Lakes system. Again, this suggests dispersal north from the Missouri system. However, this northward spread must have occurred later than that of the goldeye (probably after the draining of Lake Agassiz) since *Platygobio* is absent from northern Ontario.

Five Mississippi species (*C. artedii, N. hudsonius, P. omiscomaycus, P. fluviatilis,* and *S. vitreum*) are present in the upper Mississippi system, but are apparently absent from, or at least not native to, the upper Missouri. In our area *N. hudsonius, P. fluviatilis,* and *S. vitreum* are restricted to the Mackenzie system. These species probably spread from the upper Mississippi system into Lake Agassiz by way of the Warren River outlet, and from there north into the Mackenzie system. The trout-perch (*Percopsis omiscomaycus*) dispersed in a similar manner, but it is also present in the Yukon system. Its absence from the Tanana and upper Yukon rivers suggests that it has only recently entered the Yukon from the Peel River (Mackenzie system) and may still be spreading within the Yukon system. The ciscoes of the *C. artedii* complex presumably also spread north from the upper Mississippi through Lake Agassiz. However, they probably followed the retreating ice sheets more closely than did most other species, and as a result are more widespread in our area than are the other Mississippi forms. *Perca fluviatilis* is also present in Eurasia, but its North American range has been attained postglacially only from the Mississippi.

The two remaining Mississippi species (*C. clupeaformis* and *C. ricei*) are absent from both the Missouri and upper Mississippi systems. However, their presence in the Great Lakes and Saskatchewan River systems suggests dispersal from the upper Mississippi Valley. *Coregonus clupeaformis* is widespread in the north and has apparently reached the headwaters of the Yukon River. In our area *C. ricei* is restricted to the Mackenzie and Thelon systems. The headwaters of these rivers interdigitate in low areas and *C. ricei* probably entered the Thelon River from the Mackenzie.

Many species of Mississippi origin have been blocked from reaching the headwaters of the Liard River by rapids; nine such species occur below but not above the Liard Canyon in British Columbia.

(D) Fishes in our Area that Survived Glaciation in More than One North American Refuge

Many species now found in our area probably survived in more than one glacial refuge. In some the range still includes several possible refuges; in others the pattern of geographic variation in morphology suggests a multiple origin.

Species surviving in more than one refuge may have shown genetic divergence even at the start of Wisconsin separation, due to the effects of earlier glaciations. Divergence between isolated segments of each species during the Wisconsin was probably enhanced by climatic differences, particularly between the Bering and the two southern refuges. And even within each major refuge there may have been isolated refuges wherein further subdivision occurred. The Wisconsin ice mass was therefore bordered by highly disjunct stocks of fish. After ice withdrawal each stock could re-invade the newly exposed areas. In some species (*S. alpinus, L. lota, P. pungitius, C. cognatus*) the different forms have since come in contact and established a zone of intergradation. In others (*O. eperlanus, G. aculeatus,* and perhaps *P. cylindraceum*) the ranges of the different forms are still disjunct and there has probably been no postglacial exchange between them.

Twenty-one of the species in our area probably survived glaciation in more than one North American refuge. These are: *Prosopium cylindraceum, Prosopium coulteri, Thymallus arcticus, Salvelinus namaycush, Salvelinus alpinus, Salvelinus malma, Oncorhynchus nerka, Oncorhynchus kisutch, Oncorhynchus tshawytscha, Oncorhynchus keta, Oncorhynchus gorbuscha, Osmerus eperlanus, Esox lucius, Couesius plumbeus, Rhinichthys cataractae, Catostomus catostomus, Lota lota, Pungitius pungitius, Gasterosteus aculeatus, Myoxocephalus quadricornis,* and *Cottus cognatus.*

Six of these species (*S. malma* and the five species of *Oncorhynchus*) probably survived glaciation both in the Bering and in the Pacific refuges. The range of the Dolly Varden (*S. malma*) includes both refuges, and the existence of two distinctive morphological forms further suggests survival in two places. In our area the Pacific form of *S. malma* (see "Taxonomic Notes" for this species) is present in the upper Athabasca, Peace, Liard, and Yukon rivers as well as in coastal drainages on the Alaska Peninsula. The Dolly Varden is anadromous and probably spread north both by inland and coastal routes. The Bering form of *S. malma* is known only from scattered populations within the Bering refuge and apparently has not expanded its range postglacially.

All five species of Pacific salmon (*Oncorhynchus nerka, O. kisutch, O. tshawytscha, O. keta,* and *O. gorbuscha*) that occur in our area are widely distributed elsewhere. Their ranges include more than one unglaciated area, so they probably survived glaciation in more than one refuge. However, *Oncorhynchus* are capable of rapid dispersal; the possibility that they attained their present North American distribution by postglacial dispersal from a single refuge cannot be entirely ruled out. All occur in Asia, but only two species (*O. keta* and *O. gorbuscha*) are reliably recorded from the Arctic Ocean. Both have spread east along the arctic coast to the Mackenzie system, and *O. keta* ascends this river to the rapids at Fort Smith. One species (*O. nerka*) occurs in its landlocked form (called kokanee) in Arctic Lake in the extreme headwaters of the Peace system, probably due to recent exchange between the Peace and Fraser systems. Other than this the Pacific salmon stocks in our area may each have originated solely from the Bering rather than the Pacific components of each species.

Two species (*S. alpinus* and *O. eperlanus*) survived glaciation both in the Bering and the Atlantic refuges. Since ice retreat *S. alpinus* has re-established a continuous distribution. Within the Bering refuge it may have survived not only in the main Bering area but also in unglaciated portions of the Kodiak Island–Cook Inlet area, from whence it spread into Bristol Bay. The slightly different form that survived in the main Bering refuge spread east along the arctic coast, where it met and intergraded with an Atlantic form that had dispersed north along the Labrador coast and then west into Hudson Bay and the Arctic Archipelago.

The boreal smelt (*O. eperlanus*) also survived glaciation in the Bering and Atlantic refuges, and is represented in each area by a distinctive morphological form (see "Taxonomic Notes" under this species). The range of the two forms is disjunct; only the Bering form occurs in our area. *Osmerus eperlanus* now extends far southward into the Pacific as far as Korea, so it may have survived glaciation in the Asian Pacific, instead of, or as well as, in the Bering refuge. The anadromous form of *O. eperlanus* lives most of its life in the sea, and postglacially has spread from the Bering refuge in two directions: eastward along the arctic coast to Bathurst Inlet, and south along the Pacific coast to Barclay Sound on Vancouver Island. The Atlantic form has spread northward only to the southern coast of Labrador.

Only one of our species, the threespine stickleback (*G. aculeatus*), survived both in the Pacific and Atlantic refuges. The North American range of *G. aculeatus* is disjunct along the arctic coast, and includes three possible refuges: the Atlantic, the Pacific, and the Bering. The southern distribution along both the Atlantic and Pacific coasts indicates survival both in Atlantic and Pacific refuges. If *G. aculeatus* also survived in the Bering refuge, which is questionable, then it has not expanded its northern range postglacially, as it is restricted, at least in its freshwater form, to the southern portion of the Bering refuge; in contrast, the Atlantic population has expanded northward along the coasts of Labrador, Hudson Bay, and Baffin Island. In most areas *G. aculeatus* occurs in two forms that may best be regarded as distinct species (see "Taxonomic Notes" under *"Gasterosteus aculeatus"* complex). Apparently the freshwater form has arisen postglacially from the marine form in many separate areas.

Five species in our area (*P. cylindraceum, T. arcticus, S. namaycush, E. lucius,* and *P. pungitius*) probably survived glaciation both in the Bering and Mississippi refuges. Of these the lake trout, *S. namaycush,* is unique in that it is the only one of this group of wide-ranging species that is absent from Siberia. Since the Bering refuge included the extreme eastern tip of Siberia, Walters (1955) believed that the absence of the lake trout from this part of Siberia means that it was not present in the Bering refuge during glaciation. However, Lindsey (1964) presented arguments in favour of multiple refuges for the lake trout, and concluded that it probably survived glaciation both in the Bering and Mississippi refuges.

The ranges of three species (*T. arcticus, E. lucius,* and *P. pungitius*) still include parts of both the Mississippi and Bering refuges. In addition all three species have what appear to be distinctive Bering and Mississippi forms (see "Taxonomic Notes" under these species). In the first two species geographic variation has been examined only cursorily, but similar patterns emerge. In each, the Bering form is apparently confined to the general area of the Bering refuge, except for some postglacial dispersal southward into the Liard and Taku rivers (*E. lucius*) and some Pacific drainages south to the Taku (*T. arcticus*). The Mississippi form of each species is present in the Mackenzie system and most of the major drainages to the east. *Esox lucius* is known from the Anderson, Coppermine, Thelon, Dubawnt, and Kazan rivers, whereas *T. arcticus* is probably present in all the rivers and lakes of the Barren Grounds.

Geographic variation in the ninespine stickleback, *P. pungitius,* has been studied in detail by McPhail (1961). There are distinct Bering and Mississippi forms; the former readily enters the sea and has dispersed mainly through coastal waters. The Mississippi form appears to be less tolerant of sea water and has dispersed only through inland routes. The Bering form has spread in two directions: south into the Gulf of Alaska, and east along the arctic coast to Hudson Bay and then south down the Atlantic coast. The Mississippi form has spread north from the upper Mississippi system through glacial Lake Agassiz to the Mackenzie system, and from there into the Anderson, Coppermine, Thelon, Dubawnt and Kazan rivers. The Bering and Mississippi forms of *Pungitius* appear to intergrade in the Mackenzie Delta region and in the Back River.

The round whitefish, *P. cylindraceum,* also has two distinctive morphological forms that suggest survival both in the Bering and Mississippi refuges (see "Taxonomic Notes" for this species). The range of the two forms may still be completely separated. The Bering form dispersed south into the Liard River and Pacific drainages south to the Taku River, and also east to the Mackenzie system and then across the Barren Grounds and south at least to the Churchill River. The Mississippi form has apparently not spread beyond northern Ontario in the west, but has dispersed much farther to the north in Labrador.

Four of the species (*P. coulteri, C. catostomus, L. lota,* and *C. cognatus*) may have survived glaciation in three refuges, the Pacific, Bering, and Mississippi. The ranges of both *L. lota* and *C. cognatus* include parts of all three refuges. In addition, both species have quite distinct Bering and Mississippi forms, and an intermediate form in the area of the Pacific refuge. The intermediate nature of the Pacific forms may indicate a common mode of preglacial origin. Each successive glaciation during the Pleistocene may have fragmented the ranges of these species and produced differentiation. During each successive interglacial period a continuous range was re-established through postglacial dispersal, and a zone of intergradation developed in the area of contact. At present the area of contact for these species, and therefore the zone of intergradation, is in the Mackenzie system. If a similar situation also existed during previous interglacial periods, then the expanding glaciers would probably have pushed intermediate populations to the southwest into the Pacific refuge and perhaps also the upper Missouri region.

In our area the Bering form of *Lota* is found throughout the old Bering refuge and has spread south into the upper Liard River and Pacific drainages south to the Alsek River. The Mississippi form is found in all of the major rivers on the Barren Grounds and presumably spread north from the Mississippi refuge. Throughout the Mackenzie system the burbots appear to be intergrades between the Bering and Mississippi forms.

Geographic variation in the slimy sculpin (*C. cognatus*) has been analysed by McAllister and Lindsey (1961), who conclude that this species entered our area from the Bering, the Mississippi, and perhaps the Pacific refuges. If *C. cognatus* survived in the Pacific refuge, the populations in the upper Peace River represent the maximum penetration of the Pacific form into our area. The Bering form of *C. cognatus* probably dispersed south to the Liard River and to Pacific drainages south as far as the Stikine River, and also east into the lower Mackenzie River and the northern Barren Grounds. The Mississippi form of *C. cognatus* spread north from the upper Mississippi into the Mackenzie, Thelon, Dubawnt, and Kazan rivers. The Bering and Mississippi forms of *C. cognatus* apparently intergrade in Great Slave Lake and in some river systems on the west coast of Hudson Bay.

The pygmy whitefish, *P. coulteri,* has a wide but scattered distribution in the northwest, and is also known from Lake Superior. In our area it is recorded from the Peace, Liard, Yukon, and Alsek systems, as well as Bristol Bay drainages in Alaska. Most of its range lies within glaciated areas. This distribution was probably primarily attained through northward dispersal from the Pacific refuge, although the Bristol Bay populations undoubtedly represent, at least in part, a distinct Bering form of *P. coulteri* (see "Taxonomic Notes" for this species). Since the pygmy whitefish is absent from the many apparently suitable northern lakes east of the Rocky Mountains, it is unlikely that the populations that survived in the Mississippi refuge spread farther north than Lake Superior.

The range of the longnose sucker (*C. catostomus*) also includes the Bering, Mississippi, and Pacific refuges. The presence of this species on the Chukotsk Peninsula, Siberia, indicates survival in the Bering refuge, and relict populations in the Mississippi system and western Washington indicate survival in the Mississippi and Pacific refuges. There is also an indication that slightly distinctive morphological forms dispersed from each refuge (see "Taxonomic Notes" for this species). The Bering form of *C. catostomus* apparently has spread south into Pacific drainages and the upper Liard River, and perhaps also into the upper Peace and Fraser systems. The Mississippi form of longnose sucker ranges north to the Mackenzie Delta, and is present in most of the large rivers on the Barren Grounds. Since *C. catostomus* is present both in the upper Missouri and upper Mississippi systems, it probably dispersed north from both areas, but because of the pattern of deglaciation probably first entered our area from the upper Missouri River.

The distribution of two species, the longnose dace (*Rhinichthys cataractae*) and the lake chub (*Couesius plumbeus*), suggests that they entered our area from both the Pacific and Mississippi refuges. The distribution of each includes both refuges. Morphological divergence probably exists in each species, between Pacific and Mississippi forms, but has yet to be analyzed in detail. Both species were probably present both in the upper Missouri and the upper Mississippi, but due to the pattern of deglaciation on the Great Plains they probably first entered our area from the upper Missouri. In our area the Pacific form of *C. plumbeus* is restricted to the upper Peace River, which it apparently entered from the Fraser River. *Rhinichthys cataractae* probably also entered from the Fraser to the upper Peace River, as well as entering the Mackenzie from the Missouri system farther east. In our area *R. cataractae* is restricted to the Mackenzie drainage. The Mississippi form of *C. plumbeus,* however, ranges north to the Mackenzie, Anderson, Thelon, Dubawnt, and Kazan rivers, and is the only cyprinid to have penetrated the Yukon River in Alaska.

The remaining species, the fourhorn sculpin (*M. quadricornis*), is unique among our fishes in that it occurs both as marine and as purely freshwater populations in our area. The freshwater populations of *M. quadricornis* in our area are derived from two sources: the Mississippi refuge and the Arctic Ocean. Those derived from the Mississippi refuge are morphologically distinct and are recognized by McAllister (1961) as a different species, *Myoxocephalus thompsoni* (see "Taxonomic Notes" for this species). They probably dispersed north in the series of large proglacial lakes formed by the retreating Laurentide ice sheet. The populations of *M. quadricornis* in certain lakes on Victoria Island are intermediate between *M. quadricornis* and *M. thompsoni* in some characters. Since these lakes were postglacially inundated by the sea these populations represent recent marine relicts.

SUMMARY OF DISPERSAL ROUTES

About 27 species entered our area from the Bering refuge in whole or in part. Their dispersal routes are suggested in Fig. 4. Some probably entered the Mackenzie

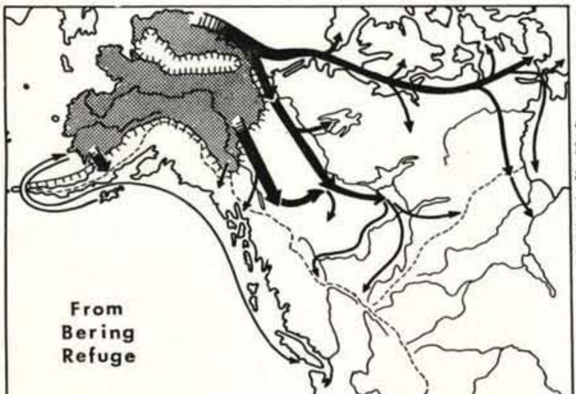


Fig. 4. Dispersal routes of about 27 freshwater fish species that entered our area wholly or in part from the Bering refuge. Width of lines roughly proportional to number of species supposedly using each dispersal route. Area of refuge stippled.

River system by headwater transfer from the Yukon River system; others entered the Mackenzie mouth from the sea. Bering species contribute heavily to fauna of the lower Mackenzie, but only lightly to the upper (upstream of Great Slave Lake). The Canadian Arctic Archipelago received most of its few freshwater fishes from the Bering refuge. Fishes of the northern Barren Grounds are predominately of Bering origin, with an increasing admixture of Mississippi forms towards the south. Some Pacific coast drainages from the Taku River north and west have received Bering species from the Yukon River; Pacific drainages from the Nass River south are free of Bering invaders other than *Osmerus eperlanus*.

Mountainous terrain separates headwaters of the Yukon River from those of the Mackenzie or of the short Pacific rivers. Where watersheds abut in such country, swift erosion or damming by slides or by beavers frequently reverses the flow of headwaters. Ice tongues from mountain glaciers may create temporary lakes in narrow valleys even in recent times. Still greater watershed instability must have existed during withdrawal of Pleistocene glaciation, creating ample opportunities for cold-adapted fish species to escape south and east from the Bering refuge. The present southeastern limits of many of these species seem not to be related to modern watershed barriers. Failure by most Bering forms to occupy the upper Mackenzie system may be due instead to climatic barriers, or to the northward advance of warm-adapted species from the Pacific and Mississippi refuges.

About 19 species entered our area from the Pacific refuge in whole or in part. (In addition, the five *Oncorhynchus* species survived in both Pacific and Bering refuges, but whether our area contains any stocks originating in the Pacific refuge is questionable.) The principal point of entry has been into the upper Peace River basin (Fig. 5). The Prince George area of the upper Fraser River is thought to have drained

Fig. 5. Dispersal routes of about 19 species that entered our area wholly or in part from the Pacific refuge.

north into the Peace postglacially (Fig. 3). However, the northward drainage at that time was probably due to ice blockage persisting farther south along the Fraser canyon. Therefore, Pacific refuge fish probably had no opportunity to move north to Prince George until after the block was removed and the outflow to the Peace had ceased. More likely the entry of Pacific species into the upper Peace is due to a relatively recent minor headwater transfer, as few species have dispersed much farther down the Peace than to the Alberta–British Columbia border. Their spread may perhaps be checked by ecological factors related to a northern plains rather than a mountain terrain, or to the presence east of the Peace River Canyon of fish species from the Mississippi refuge that are not encountered west of the Continental Divide. Three species (*P. williamsoni, S. malma,* and *S. gairdneri*) may have crossed the Divide at more than one point, and might have entered our area in part by moving north along the eastern slope of the mountains. Only a few Pacific forms have penetrated the Bering sea drainages; of these most extend only to Bristol Bay, and none reaches the arctic coast of Canada.

About 30 species entered our area solely or in part from the Mississippi refuge (Fig. 6). The succession of southward draining temporary lakes that formed during

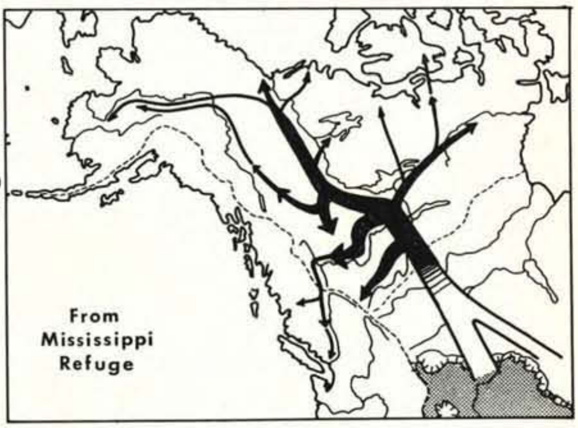


Fig. 6. Dispersal routes of about 30 species that entered our area wholly or in part from the Mississippi refuge.

retreat of Wisconsin glaciation (Fig. 3) provided ready access into central Canada from the south. Most fish species in the upper Mackenzie are of Mississippi origin. The mass of relatively warm water borne north by the huge Mackenzie River thrusts a narrow finger of temperate climate right to the Arctic Ocean; hence, even the lower Mackenzie carries in its main stem several southern forms that are otherwise confined to lower latitudes.

Many Mississippi forms have ascended the Peace River only slightly into British Columbia, where they were perhaps blocked by the Peace River Canyon (now dammed). Exchange across the Continental Divide has been less from east to west (3 or 4 species) than from west to east (perhaps 10 species or races). Mississippi species may have reached the Pacific slope via Lake Peace and temporary lakes in the Prince George basin (Fig. 3); that they have been present west of the present Continental Divide for quite a long time is indicated by their wide dispersal in the upper Fraser system and the Skeena River, suggesting early entry after first separation of the Cordilleran and Laurentide ice sheets.

Probably only two Mississippi species have reached Alaska, both by headwater transfer into the upper Yukon River basin.

The geographic limits to freshwater fishes in northern North America are only in part dictated by present watershed boundaries. These boundaries are more evanescent even in recent times than might be supposed; during glacial retreat many temporary lakes straddled modern drainage divides and afforded steps whereby fish could move from almost any drainage system to any other, provided that the fish were in the right place at the right time. Ecological rather than land barriers seem to be most important in limiting dispersal of freshwater fishes in our region. Ecological factors either are operating now to hold fish within certain portions of open watersheds (e.g. to the northern or to the southern part of the Mackenzie basin) or else have operated in the past to prevent a species from making use of paths temporarily open to new areas. We are almost totally ignorant of what these ecological factors are and of how they operate.

CLASSIFICATION AND NOMENCLATURE

It is surprising and dismaying to nonspecialists that different scientists advocate different scientific names for the same species of fish. The scientific name (usually with a Latin or Greek root) might be expected to remain as an immutable indicator of the species, unaffected by geography or language. Instead, a curious situation has arisen in North America, where common names of many fish have been stable whereas their scientific names have vacillated. The criteria used in selecting names in this Bulletin are given below.

Common Names

English common names in almost all instances follow those recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (Bailey et al., 1960). Discrepancies are due either to our recognition of subspecific categories (which are not indicated in that list) (e.g. American yellow perch), or to differences in interpretation of specific limits (e.g. we believe that the Bering cisco and Arctic cisco are different species). Common names of fishes are not capitalized except where proper names are involved such as Bering, Arctic, or Dolly Varden.

French common names have been selected in cooperation with Vianney Legendre of the Quebec Department of Tourism, Fish and Game.

Family

Families are presented in the sequence given by Greenwood et al. (1966); in only two instances do our family names or limits differ (Salmonidae, Dalliidae).

Genus

The name of a genus must be changed if it is discovered that the name had been assigned previously to some other animal. An example is the brook stickleback; the genus *Eucalia* turned out to have been applied earlier to a butterfly, so a new name *Culaea* was coined for the fish, now *Culaea inconstans*.

Most changes of generic name, however, result from changing opinions as to the degrees of relatedness between species. A primary purpose of the genus is to indicate that all species within that genus are more closely related to each other than to any other species. The argument arises between "lumpers" on the one hand, who seek large comprehensive genera "that assemble, and thereby underscore, some contrasting features as well as the many unifying characters to be found among intimately related organisms" (Rosen and Bailey, 1963), and "splitters" on the other hand, who wish to avoid a genus so large that it gives no clue about relationships amongst its many members. For example, "lumpers" argue that similarities between the lake trout and other chars in the genus *Salvelinus* should be stressed by calling the lake trout *Salvelinus namaycush;* "splitters" argue that its distinctiveness among this group of fishes should be emphasized by the name *Cristivomer namaycush*. Detailed arguments have been advanced for both actions; this is a borderline case, which must be decided by each scientist for himself. In general we favour the expanded genus provided it is based on sufficient published knowledge.

Unfortunately some proposed changes have not been supported by published documentation. In these instances we believe that the usefulness and reputation of fish taxonomy would be enhanced by greater conservatism. *Scientific names should be altered reluctantly, and only in the face of convincing published evidence.* On this basis we have accepted the whitefish genus *Prosopium* as distinct from *Coregonus,* and have rejected the genus *Leucichthys*; careful morphological studies on which to base these actions have been presented by Norden (1961). We also accept the lumping of *Margariscus* with *Semotilus* on the basis of published argument (Bailey and Allum, 1962). On the other hand, we reject recent suggestions that the minnow genera *Pfrille, Platygobio,* and *Couesius* be lumped with other genera, because we know of no published arguments to support such changes. As an example of the disservice that piecemeal name changes can do to nomenclatural stability, the finescale dace *Pfrille neogaea* has recently been moved to the genus *Chrosomus* (which it undoubtedly resembles in many ways). But even while the new name *Chrosomus neogaeus* is being learned by nontaxonomists, a further suggestion is current that both *Pfrille* and *Chrosomus* should be lumped with the Old World genus *Phoxinus,* in which instance the finescale dace would become *Phoxinus neogaeus* (which was its original name in 1866). In place of these fragmentary changes, we urge that generic names be altered only as a result of published studies of all the species that might be involved. Further discussion will be found throughout this bulletin in the "Taxonomic Notes" sections of species involved in possible name changes.

In zoology, the name of the genus is always capitalized, that of the species never.

Species

The decision whether to "lump" or "split" two related forms can rely on a firmer criterion at the specific than the generic level. If two morphologically distinguishable forms occupy the same water (i.e. are sympatric) but do not successfully interbreed with each other, they are generally considered to be two distinct species. This criterion of "reproductive isolation" is not without difficulties, as for example when occasional fertile hybrids appear between two usually distinct forms. But even in localities where some fertile hybrids do occur the majority of individuals often fall into two clearly separable groups that seem to have preserved their gene pools "uncontaminated" (as demonstrated for *Gasterosteus* by Hagen (1967), and *Catostomus* by Nelson (1968a)). How this happens is still an evolutionary puzzle. Moreover, in our area, with its complex glacial history, there may be pairs of forms that do successfully interbreed in some lakes although remaining distinct in others. In all these instances, we believe that two forms that occur sympatrically in *any* locality without introgression (i.e. without successful exchange between the two gene pools) are most conveniently treated as two distinct species; intermediate populations arising by introgression can then be labelled as hybrids between these two species. Where two forms are wholly allopatric the criterion of reproductive isolation cannot be tested; here perhaps morphological separability of 100% of the individuals in both samples on the basis of one or preferably several genetically based characters should be required as an indication of two distinct species.

We have applied the criterion of reproductive isolation where enough information is available (e.g. *Salvelinus malma* and *S. alpinus*). But in several instances there are insufficient data to decide whether one or several species are involved. In these we have resorted to terms such as " '*Coregonus clupeaformis*' complex," which emphasizes the existence of an unresolved problem. Detailed discussions appear under individual "Taxonomic Notes."

Changes in spelling of specific names arise from internationally agreed rules of nomenclature (Stoll, 1961). Many specific names are in the form of adjectives whose Latinized endings must agree with the gender of the genus. Thus in the example given previously of a change in genus of the finescale dace, *Pfrille* is feminine and the appropriate specific name is *neogaea,* but *Chrosomus* and *Phoxinus* are masculine, so the species name if moved to either of these genera would be spelled *neogaeus.*

Specific names based on persons (e.g. *Salmo gairdneri,* after Dr Meredith Gairdner) are sometimes spelled with a double *i* ending (*gairdnerii*). No clear international agreement has been reached. As spelling is at present optional, we have elected the simpler spelling throughout. In this Bulletin only *Coregonus artedii* has an *ii* ending, formed by adding a single *i* to the name of Petrus Artedi.

Subspecies

In deciding whether or not to recognize subspecies, we have followed the principles given by Bailey et al. (1954, p. 148). "A species should not be divided into subspecies on the basis of clinal type variation . . . A species is properly divisible into subspecies when data have been suitably published to demonstrate that it consists of two or more allopatric populations, each displaying a high degree of uniformity over its range and differing with high constancy (a figure of at least 93% of individuals is suggested) from other forms, each of which intergrades over a relatively narrow geographic area with at least one other form."

On this basis, we recognize only a few subspecies in this Bulletin. Quite a few other species show within our area morphological differentiation probably arising from isolation in two or more glacial refuges (e.g. *Catostomus catostomus, Pungitius pungitius*). These instances fulfill all of the stated requirements except that of degree of difference; most *populations* can be assigned to northern or southern types on the basis of the proportion of individuals showing a given character, but attempts to assign *individuals* are much less successful. Moreover, there is often a wide area of intergradation within which even populations are intermediate. Formal recognition of these northern and southern types as subspecies may be justified in the future when greater taxonomic precision has been reached, but at present it does not seem useful.

AUTHOR

The name of the author who first described the species or subspecies is usually shown following the species or subspecies, although it is not a necessary part of the scientific name. If the genus presently used differs from that given in the original description, the author's name appears in parentheses; for example, *Salmo alpinus* Linnaeus became *Salvelinus alpinus* (Linnaeus).

SCOPE OF SPECIES DESCRIPTIONS

Each major fish illustration (except those of Pacific salmon) was drawn by Mrs Jean Ramsey Maher from a preserved specimen collected in our area, using as a guide a projected photograph of the specimen. Usually only a sample patch of scales was drawn. All specimens used for major illustrations were adults; young may differ considerably from these in pigmentation and body proportions (and usually have a proportionally larger eye than adults). Illustrations in the keys were drawn from preserved fish by C. C. Lindsey using a camera lucida.

The large distribution maps show localities from which we have examined specimens, and those from which there are reliable published records. They include only records from within the area indicated in the "Introduction" (lying north of the broken line on the distribution map). The small inset maps show the known total natural distribution of the species throughout the world. Introductions of a species beyond its natural range are omitted (except in *Salvelinus fontinalis*).

Distribution records and descriptions, although supplemented from published accounts, are based largely on examination of fish collections in the University of British Columbia, the Royal Ontario Museum, the National Museums of Canada, the United States National Museum, the Museum of Zoology of the University of Michigan, and Stanford University.

Only recommended common names are given in the heading for each species. Alternative common names are sometimes mentioned at the end of the "Biology" section.

Under the scientific name an explanation appears of the roots from which the name was derived.

"Distinguishing Characters" summarizes those salient points given in the keys and descriptions that separate that species from its near relatives in our area.

The "Description" is for the species as a whole, excepting that where we are aware of significant differences between specimens from our area and elsewhere these have been noted. Explanations of technical terms may be found in the following section, and in the Glossary on p. 34.

Statements of "Distribution" outside of the area covered in this Bulletin are largely assembled from the literature (particularly from Hubbs and Lagler, 1964), supplemented occasionally by records in the museum collections listed above.

"Taxonomic Notes" does not attempt to list all synonyms for a species, but refers to the original description and to certain synonyms likely to be encountered. These are followed by a discussion of certain taxonomic problems in our area.

"Postglacial Dispersal" summarizes the probable pattern whereby the species has reached its present distribution from refuges at the margin of Wisconsin glaciation. Refuge areas and dispersal routes during glacial recession are described in the introductory chapters "Outline of Geological History," "Zoogeographic Patterns," and "Summary of Dispersal Routes."

"Biology" includes available information on habitat, food, growth, reproduction, and economic value. When no data are available from our area, information is sometimes included concerning the same species from elsewhere and is so indicated.

METHODS OF IDENTIFYING FISHES

Technical terms used in the keys and in the species descriptions are explained in the "Glossary." For characters commonly used in identification a more detailed explanation follows.

Body proportions are measured from point to point with a ruler or calipers, or are stepped off with dividers. The size of a part (such as head length) is usually expressed in terms of a larger measurement, as a proportion, a fraction, or a percentage (e.g. "head 4 times into length," or "head ¼ length," or "head 25% of length," are all equivalent). In statements of proportion, "length" refers to standard length of the body unless otherwise stated; other body measurements are described in Fig. 7 and in the "Glossary."

Counts of spines and of fin rays are given separately. Spines are needlelike structures that have a sharp and rather stiff point and no branching or segmentation; rays are softer, often with one or more branches at the soft expanded tip, and are jointed, like bamboo (Fig. 7). Most soft rayed fins have a relatively straight leading edge; in these only the *major* or *principal rays* are counted, not the very small 1–3 rudimentary rays at the front (the longest of which is less than one-half the length of the first major ray) (Fig. 7). Thus, in the families Hiodontidae, Coregonidae, Salmonidae, Osmeridae, Cyprinidae, and Catostomidae the count of the major rays is one greater than the count of branched rays, as the first major ray is unbranched. In other families in this Bulletin the total count of all soft rays is given. In all families the last two soft rays at the posterior of the dorsal or anal fin are counted as one if their bases are notably closer together than are the bases of the other rays (Fig. 7).

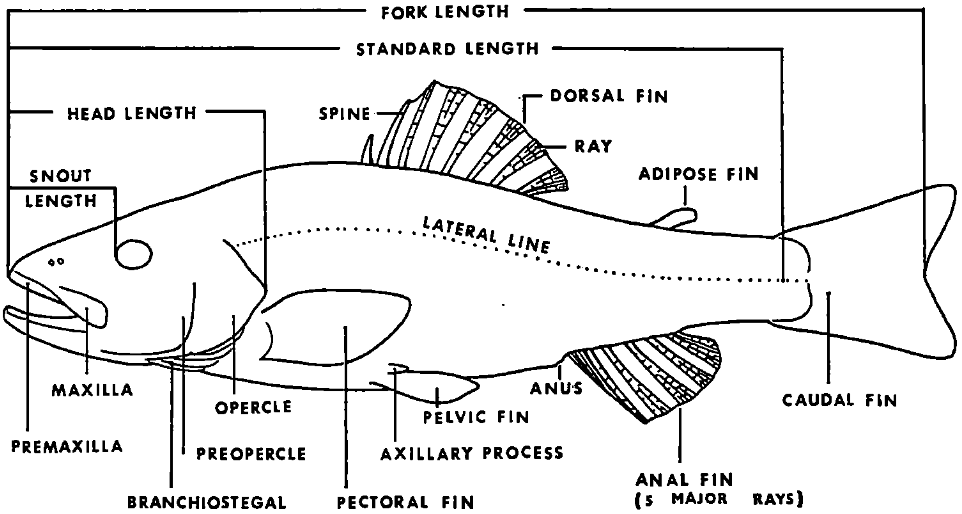


Fig. 7. Imaginary fish, illustrating external parts and measurements.

Lateral line scales refers to the number of pores in the lateral line, or to the number of scales along the line in the position usually occupied by a lateral line. The first scale counted is that one in contact with the bony shoulder girdle. Unless otherwise specified, *lateral line scale* counts terminate at the caudal flexure. However, number of *pores in the lateral line* refers to *all* pored scales including any lying posterior to the caudal flexure.

Scale rows around the caudal peduncle refers to the numbers of horizontal rows crossing an imaginary line around the narrowest part of the caudal peduncle (Fig. 15).

Scale rows above the lateral line are counted from the origin of the dorsal fin downward and backward following the natural scale row to but not including the lateral line.

GLOSSARY

GLOSSARY

Adipose eyelid — transparent tissue around margin of eye (Fig. 13).

Adipose fin — a small fleshy rayless fin on the back between the dorsal and caudal fins (Fig. 7).

Allopatric — living in geographically separated places (in contrast to Sympatric).

Ammocoete — the blind wormlike larva of the lamprey.

Amphipods — crustaceans belonging to the family that includes freshwater shrimps.

Anadromous — ascending rivers from the sea to spawn.

Anal — referring to the anus or vent.

Anal fin — the ventral unpaired fin (Fig. 7) just ahead of the caudal peduncle.

Annulus (plural *Annuli*) — a mark formed on a fish scale each year, often in late winter.

Anterior — the front portion; in front.

Axillary process — a triangular scalelike projection lying in the angle between the base of the pectoral or pelvic fin and the body (Fig. 21).

Barbel — a slender flexible projection near the mouth, usually provided with taste or touch receptors (Fig. 20, 22, 23).

Barren Grounds — the largely treeless area or tundra between Hudson Bay on the east, and Great Slave and Great Bear lakes on the west, and from about 59°N to the Arctic Ocean.

Basibranchials — the three median bones in the floor of the gill chamber, grasped by the ventral ends of the five gill arches.

Basihyal — the median bone whose rear end joins the basibranchials and whose free front end forms the "tongue" in the floor of the mouth.

Benthic — living on or near to the bottom (in contrast to Pelagic).

Bicuspid — having two points.

Bifid — divided into two parts by a cleft or notch.

BP — refers to the number of years before the present time.

Branchiostegals — the bony struts that support the membrane lying below the gill cover (Fig. 7).

Breast (of a fish) — ventral surface ahead of the pelvic fins.

Caecum (plural *Caeca*) — a blind sac.

Canine teeth — conical teeth that project beyond the others (Fig. 26B).

Caudal fin — tail fin (Fig. 7).

Caudal flexure — the structural base of the caudal fin, as indicated by the position of the crease formed when the caudal fin is flexed from side to side. Usually a few scales extend behind the caudal flexure.

Caudal peduncle — the wristlike region of the body behind the anal fin and ahead of the caudal fin.

Chironomids — flies belonging to the midge family.

Cladocera — a group of small crustaceans called water fleas, which include *Daphnia.*

Class — a major grouping of animals, containing several Orders, each of which contains Families etc.

Cleithral spines — those arising from the pectoral girdle just above the base of the pectoral fin.

Cline (adjective *Clinal*) — progressive change or gradient in structure or feature of animals that follows a geographic gradient such as latitude or altitude (e.g. increase in number of fin rays in a species northwards).

Complete lateral line — one in which the row of lateral line pores extends back at least as far as the caudal flexure.

Compressed — flattened from side to side.

Concave — curved inward, hollowed.

Continental Divide — used here to indicate the watershed boundary, generally following the Rocky Mountains, that separates Pacific coast drainages from other major drainages in northern North America.

Convex — curved outward, arched.

Crustaceans — members of the large class Crustacea of the phylum Arthropoda (all of which have a hard jointed external skeleton), including shrimps, crayfish, and water fleas.

Ctenoid scales — scales bearing teeth or prickles on the exposed (posterior) margin.

Cycloid scales — oval or smoothly rounded scales having no prickles.

Deciduous — shed periodically or with age.

Decurved — bent downwards.

Dentary — large paired bones forming the front of the lower jaw.

Denticulated — having fine toothlike projections.

Depressed dorsal fin length — distance from front of fin base to tip of longest ray when fin is held flat against the body.

Depth — the vertical distance through, as of the body of fishes.

Dimorphism — existing in two forms.

Dorsal — pertaining to the back; often used as an abbreviation for dorsal fin.

Dorsal fin — the fin or fins on the back that bear spines or rays (Fig. 7).

Ecology (adjective *Ecological*) — study of the relationships of animals and plants to their surroundings, both animate and inanimate.

Esker — a ridge of gravel left by glacial action, perhaps representing the bed of a river that ran beneath the ice.

Eye diameter — the greatest distance between opposite margins of the orbit or eye socket (in contrast to iris diameter, which is the distance across the black aperture in the centre of the eye).

Falcate — sickle shaped; with a concave margin.

Family — one of the kinds of groups used in classifying organisms. Consists of a number of Genera (or only one Genus). Similar Families are grouped in an Order. Animal family names end in *-idae.*

Fauna — the assemblage of animals inhabiting a region.

Fish (plural *Fish* (for many of one kind) or *Fishes* (usually referring to several different species)) — a cold-blooded vertebrate animal having gills throughout life and with limbs, if present, in the form of fins.

Fork length — distance from the tip of snout or upper lip to tip of middle ray of the caudal fin (Fig. 7).

Frontal spines — those lying on the head between the posterior margins of the eyes.

Gasbladder (also called *Swimbladder* or *Air bladder*) — a membranous gas-filled sac in the upper part of the body cavity.

Gastropods — a class of molluscs, including snails and slugs, usually with coiled shells.

Genital papilla — a projection near the anus that carries the external opening of the reproductive system.

Genotypic — refers to hereditary characteristics (in contrast to Phenotypic characters that are the direct result of the environment modifying the individual).

Genus (plural *Genera*) — one of the kinds of groups used in classifying organisms. Consists of a number of similar Species (or a single Species). For discussion see p. 26.

Gill arches — the V-shaped bony supports bearing the gills and gill rakers (Fig. 11).

Gill rakers — a series of bony projections along the anterior edge of the gill arch. Gill-raker counts are made on the left anterior arch. Every raker is counted, including those bony rudiments at the ends of the series that may be difficult to see except under magnification. Often the count is given in two parts, upper and lower (the latter including that raker that lies in the angle of the arch) (Fig. 11). Thus a gill-raker count of 5–9 + 12–15 means that there are from 5 to 9 rakers on the upper part of the arch and from 12 to 15 on the lower. The length of the longest gill raker (usually lying just below the angle of the arch) is measured with calipers from the tip to the acute angle at the ventral side of the raker base.

Head length — distance from the most anterior point of the snout or upper lip to the posterior edge of the membrane of the opercle (Fig. 7).

Hypsithermal period — the period from roughly 7000 to 4500 years ago, when the climate was warmer than at present.

Hypurals — expanded ventral processes on the last few vertebrae, forming the bony base of the caudal fin.

Ichthyology — the scientific study of fishes.

Illinoian glaciation — the second-last (and the most extensive) ice sheet, which covered part of North America roughly 300,000 years ago.

Immaculate — without spots or pigment pattern.

Incomplete lateral line — one in which the row of pores along the side does not extend back as far as the caudal flexure.

Infraoral — below the mouth; in lampreys refers to the teeth below the opening to the pharynx (Fig. 8A).

Interorbital distance — the narrowest distance across the head between the bony edges of the eye sockets.

Isostatic rebound — slow rise in part of the earth's crust, perhaps after removal of the weight of an ice sheet.

Isthmus — the fleshy space beneath the head and between the gill openings (Fig. 24A).

Keeled — having a hard sharp ridge.

Larva (plural *Larvae*) — the young of an animal that differs markedly from the adult.

Lateral line — a sensory system on the side of the body usually consisting of a canal below the skin that opens to the surface through pores (Fig. 7). See comments on counting methods preceding this Glossary.

Laterally compressed — flattened from side to side.

Lateral tooth plates — in lampreys, those tooth plates lying on either side of the opening to the pharynx (Fig. 8A).

Lingual — related to the tongue.

Littoral — inhabiting the bottom of the sea or a lake near the shore.

Maxilla (plural *Maxillae*; also called *Maxillary*) — the bones, one on each side of the upper jaw, lying immediately above or behind, and parallel to, the premaxilla (Fig. 7). The length of the upper jaw is the distance from the tip of the snout to the hind margin of the maxilla.

Median — lying in the midline that divides an animal into right and left halves.

Melanophore — black pigment cell.

Metamorphosis — period of rapid transformation from larval to adult form.

Mode (adjective *Modal*) — the most commonly occurring count or value.

Molar — with a flattened grinding surface.

Nape — part of the body immediately behind head on dorsal surface.

Oesophagus — part of the gut between the pharynx and the stomach (Fig. 9).

Opercle — the large posterior bone of the gill cover (Fig. 7).

Orbit diameter — same as eye diameter.

Origin of fin — the point where the anterior edge of the fin meets the body.

Palatine bones — a pair of bones in the roof of the mouth behind and on either side of the median vomer (Fig. 25). Teeth on the palatine bones are sometimes concealed by mucus but can be felt by stroking with a needle point.

Papilla (plural *Papillae*) — small fleshy projection.

Parasphenoid — the long straight median bone forming the base of the fish skull, running from the vomer at the front to the basioccipital at the back.

Parietal spines — those lying on the head behind the frontal spines about opposite the preopercles.

Parr marks — dark vertical marks on the sides of young fish.

Pectoral fin — paired fin either close behind or below the gill openings, corresponding to forelimb of a mammal (Fig. 7).

Pectoral girdle — internal bony support lying immediately behind the opercular slit, attached at the top to the back of the skull and supporting the pectoral fin.

Peduncle — a stalk or wristlike base (see *Caudal peduncle*).

Pelagic — living in open water (in contrast to bottom-living Benthic).

Pelvic fin — ventral paired fin lying below the pectoral fin or between it and the anal fin (Fig. 7).

Peritoneum — membranous lining of the body cavity.

Pharyngeal teeth — bony toothlike projections from the fifth gill arch. These are small tooth-bearing plates on the roof and floor of the pharynx in most fishes, but in Cyprinidae they consist of a vertical arc of bone with the teeth projecting at right angles towards the midline. Methods of counting pharyngeal teeth are given in the introductory notes to the Family Cyprinidae. The arch, which lies behind the last gill slit, may be detached using a hooked needle or fine forceps inserted under the dorsal and ventral arms of the arch to sever the ligamentous attachments. Teeth are easily broken off while the arch is being removed; tooth counts should be made under magnification, and empty sockets or broken tooth bases included in the counts.

Pharynx (adjective *Pharyngeal*) — the first portion of the digestive tract behind the mouth.

Phenotypic — refers to characteristics that are the result of direct modification of the individual by the environment (in contrast to genotypic or hereditary characters).

Piscivorous — fish-eating.

Plankton — tiny aquatic plants and animals living above the bottom whose locomotory powers are weak compared with water currents.

Pleistocene period — the last 1 million years, during which time there were probably four major advances and retreats of ice sheets in North America.

Posterials — a U-shaped row of small teeth in the sucking disk of lampreys, connecting the lower pair of lateral tooth plates (Fig. 8A).

Posterior — behind.

Predorsal distance — from tip of snout to front margin of dorsal fin base.

Premaxilla (plural *Premaxillae*; also called *Premaxillary*) — the paired bones that form the front of the upper jaw (or, in higher spiny-rayed fishes, the entire border of the upper jaw) (Fig. 7).

Preopercle — sickle-shaped bone that forms the cheek, lying behind and below the eye and ahead of the opercle (Fig. 7).

Proglacial lake — a lake, part of whose margin is an ice sheet.

Pterygoid — paired bones in the roof of the mouth behind the palatines.

Pyloric caecum (plural *caeca*) — pouch(es) coming off the intestinal tract immediately behind the stomach. In counting, all tips of branched caeca are usually enumerated.

Ray — an articulated or jointed rod, usually branched at its tip, that supports the membranes of a fin (Fig. 7). For counting methods see paragraphs preceding this Glossary.

Redd — the gravel nest of salmonid fishes.

Refuge (or *Refugium*, plural *Refugia*) — used here to mean the ice-free areas in which fish survived around the margins of continental glaciers.

Relict (or *Relic*) — surviving organism or population, usually of restricted distribution, of a species formerly more widespread.

Respiratory tube — the median tube opening off the ventral surface of the oesophagus in lampreys that connects on either side to each of seven gill pouches (Fig. 9).

Rudimentary — poorly developed.

Scute — a bony or horny plate.

Serrate — saw-toothed.

Snout length — distance from the most anterior point of the snout or upper lip to the front margin of the eye socket (Fig. 7).

Species (the same word is either singular or plural) — groups of naturally or potentially interbreeding populations that are reproductively isolated from other such groups and are usually morphologically separable from them. For discussion see p. 27.

Spine — needlelike structure that is not branched, is without segmentation, and is more or less stiff and sharp at the end (Fig. 7).

Standard length — distance from tip of snout or upper lip to the caudal flexure (Fig. 7).

Striations — grooves or streaks.

Subopercle — bony plate immediately below the opercle in the gill cover.

Subspecies — an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species. For discussion see p. 28.

Supraoccipital crest — the posterior median ridge on the back of the skull.

Supraoral — above the mouth; refers in lampreys to the row of teeth above the opening of the pharynx (Fig. 8A).

Suprapelvic scale count — starts at the anterior-most scale showing (in part or in whole) above the dorsal free edge of the pelvic axillary process, and proceeds upward and backward to but not including the lateral line.

Sympatric — living in the same place, or at least overlapping partly in ranges. Sympatric animals, unlike Allopatric ones, are not denied the opportunity to interbreed by any geographic barrier.

Synonym — an additional scientific name for the same animal (applied when the same species has been described by two different people and given different names).

Terminal — at the end; a terminal mouth is one in which the mouth cleft reaches the anterior end and is not overhung by the snout.

Tricuspid — with three points or cusps.

Tubercle — projection or lump, often hard.

Type — term used in taxonomy referring to the first-named species in a genus ("type species"), or to the individual specimen on which a taxonomic description is based ("type specimen").

Unicuspid — with a single point or cusp.

Velar tentacle — a membranous fingerlike projection (which, in lampreys, lies at the junction of the respiratory tube and oesophagus) (Fig. 9).

Vent — the external opening of the alimentary canal; the anus.

Ventral — pertaining to the lower side; opposite to dorsal. Sometimes the pelvic fins are called the ventral fins, but this is misleading, as the anal fin is also ventral in position.

Vermiculations — wiggly marks like worm tracks.

Vertebra (plural *Vertebrae*) — a bone of the spinal column.

Vomer — the median bone on the roof of the mouth, lying behind the premaxillae and separating the paired palatine bones (Fig. 18, 25). It may bear teeth (particularly at the anterior end) that are detectable by stroking with a needle point even if they are hidden from view by mucus.

Weberian apparatus — a modification of the first four or five vertebrae in minnows, suckers, and their relatives (Ostariophysi), connecting the gasbladder to the inner ear by a chain of small bones.

Wisconsin glaciation — the most recent continental ice sheet, which covered part of North America from roughly 50,000 to 10,000 years ago.

USE OF KEYS

KEY TO FAMILIES

USE OF KEYS

To identify a fish start with the Key to Families, and after the Family is known proceed to the appropriate Key to Species. Each key consists of a series of numbered pairs of alternative statements. Start at the first. If the statement in the key fits your specimen proceed to the number indicated on the right. If a statement does not fit your specimen, proceed to the statement indicated by the alternative number in parentheses preceding the statement. Repeat the procedure until you reach an identification. When in doubt as to which statement is appropriate, follow both alternatives through, and check the illustration and description of each alternative identification to find which is correct.

The following keys are based on northern specimens and may work only for the area outlined in the "Introduction." Marine species that commonly enter fresh water, and certain freshwater species reported from nearby areas, are included in the keys, but are not illustrated or described in the text.

KEY TO FAMILIES

1(2) No paired fins, body eel-like; mouth in the form of an oval or circular sucking disk; seven external gill openings.

Lampreys
Petromyzontidae
p. 48

2(1) Paired fins present; mouth not in the form of a circular sucking disk; a single external gill opening or slit on each side 3

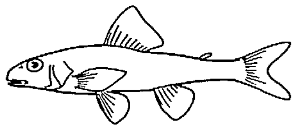
3(4) Upper lobe of tail fin much longer than lower (i.e. heterocercal); mouth ventral, with four barbels under the snout ahead of the mouth.

Sturgeons
Acipenseridae
p. 60

4(3) Tail fin not heterocercal; no barbels ahead of the mouth 5

5(14) Adipose fin present (a small fleshy tab on the back between the dorsal fin and the tail) 6

6(7) Adipose fin far behind the anal fin base; pectoral fin extends far behind the pelvic fin base.

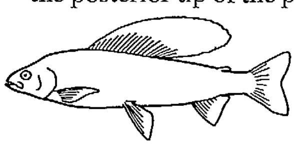


Trout-perches
Percopsidae
p. 289

7(6) Front of adipose fin lies opposite anal fin base; pectoral fins do not reach pelvic fin base 8

8(13) Pelvic axillary process present (a small fleshy appendage at the base of the pelvic fin (Fig. 7)) 9

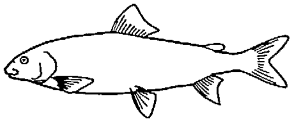
9(10) Dorsal fin large (18 or more soft rays), its anterior end lying ahead of the posterior tip of the pectoral fin.



Graylings
Thymallidae
p. 123

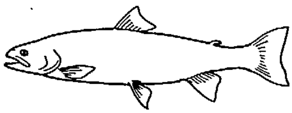
10(9) Dorsal fin smaller (15 or fewer soft rays), its anterior end lying behind the posterior tip of the pectoral fin 11

11(12) Teeth in jaws weak or absent; scales large (4–11 scale rows above lateral line).



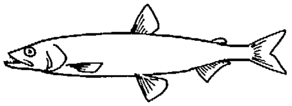
Whitefishes
Coregonidae
p. 69

12(11) Teeth in jaws well developed; scales small, difficult to count (20–27 scale rows above lateral line).



Trouts, Chars, and Salmons
Salmonidae
p. 129

13(8) Pelvic axillary process absent.



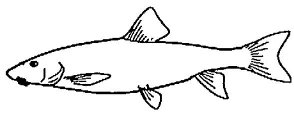
Smelts
Osmeridae
p. 187

14(5) No adipose fin 15

15(24) Pelvic fins placed far back on body, their bases overlapped only slightly or not at all by tips of pectorals 16

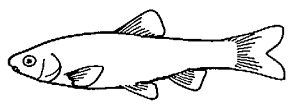
16(19) Teeth absent from mouth; front of dorsal fin less than halfway from tip of snout to tip of caudal fin 17

17(18) Mouth ventral, adapted for sucking, lips thick and covered with papillae; distance from snout to anus over $2\frac{1}{2}$ times distance from anus to base of caudal fin (caudal flexure).



Suckers
Catostomidae
p. 274

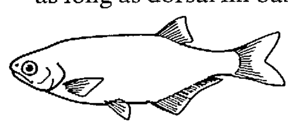
18(17) Mouth and lips without papillae; snout to anus less than $2\frac{1}{2}$ times distance from anus to base of caudal fin (caudal flexure).



Minnows
Cyprinidae
p. 216

19(16) Teeth present in mouth; front of dorsal fin distinctly more than halfway back from tip of snout to tip of caudal 20

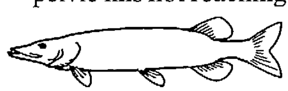
20(21) Lower jaw not protruding beyond snout; anal fin base more than twice as long as dorsal fin base.



Mooneyes
Hiodontidae
p. 63

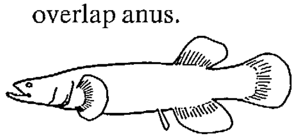
21(20) Lower jaw protrudes beyond snout; dorsal and anal fin bases roughly equal in length 22

22(23) Caudal fin forked; forehead flattened, snout like a duck's bill; tips of pelvic fins not reaching anus.



Pikes
Esocidae
p. 205

23(22) Caudal fin rounded; forehead rounded in profile; tips of pelvic fins overlap anus.

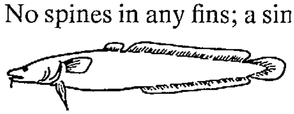


Blackfish
Dalliidae
p. 211

24(15) Pelvic fins placed forward on body, their bases opposite or ahead of centres of pectoral fins 25

25(32) Eyes are in normal position on opposite sides of head; body not flat, the animal not lying on its side 26

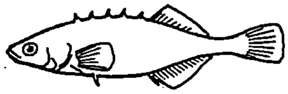
26(27) No spines in any fins; a single barbel under the chin.



Cods
Gadidae
p. 295

27(26) Spines at front of dorsal fin and in pelvics; no barbel on chin 28

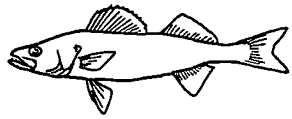
28(29) Isolated spines lying ahead of the soft dorsal fin, the spines not connected to each other by a membrane; pelvic fin reduced to a stout spine and one tiny ray.



Sticklebacks
Gasterosteidae
p. 301

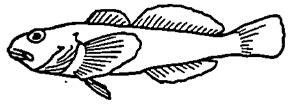
29(28) Two dorsal fins, the first containing spines united by a membrane; pelvic fin with several rays longer than the single pelvic spine 30

30(31) Body covered with distinct scales; anal fin with 1 or 2 spines.



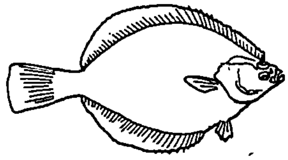
Perches
Percidae
p. 341

31(30) Body naked, or only partially covered with rows of bony tubercles or with prickles; no spines in anal fin.



Sculpins
Cottidae
p. 316

32(25) Eyes both on one side of head; body flat, the animal lying on its side.



Flounders
Pleuronectidae
p. 354

SPECIES ACCOUNTS

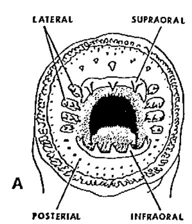
THE LAMPREYS — Family PETROMYZONTIDAE

Lampreys appear superficially like eels, but are fundamentally dissimilar. Lampreys differ from bony fishes (which include the eels) by the absence of bone, jaws, ribs, or paired fins, and by the presence of seven external gill openings and a single nostril in the midline on top of the head. They have no gasbladder. During their life cycle lampreys pass through two stages: a larval state (called an ammocoete) and an adult stage. Ammocoetes lack eyes, teeth, and a sucking disk; they live in the mud of stream bottoms and feed by straining organic material from the water diverted into the mouth by a scoop-shaped oral hood. At the end of several years the ammocoetes change into adult lampreys and emerge from the mud. Adults have eyes, and a sucking disk bearing horny teeth. In parasitic forms the adult feeds on fish and grows for a year or more before spawning. Their horny teeth and tongue are used to rasp a hole in the host's body, from which blood is sucked. In nonparasitic forms the adult does not feed; it spawns and dies a few months after leaving the mud. Adults may live in either fresh or salt water, but spawning always occurs in the gravel bottom of streams. Usually a depression is cleared among stones or gravel, into which are shed thousands of small whitish eggs. Lampreys probably do not guard their nests, and die after spawning.

The family Petromyzontidae contains about 7 genera and 30 species, in cool waters of both northern and southern hemispheres. Two species are recorded from our area, with at least two others extending north on the Pacific coast as far as southeastern Alaska.

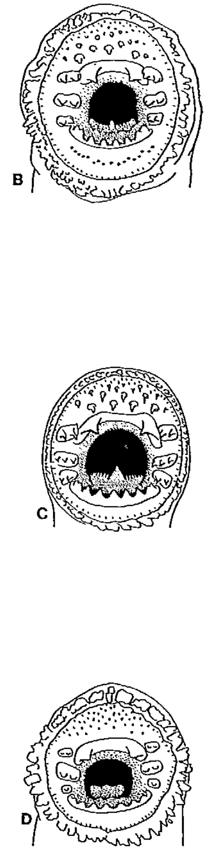
Key to Adult Lampreys, including North American Pacific species (teeth visible, eyes distinct, no oral hood)

1(2) Four pairs of lateral tooth plates, the two centre pairs each with three points; supraoral tooth bar with three sharp teeth (Fig. 8A) .... Pacific lamprey, *Entosphenus tridentatus* (Gairdner) (p. 57)



2(1) Two or three pairs of lateral tooth plates, the centre pair with two or three points; supraoral tooth bar with two teeth (very rarely, a small central third tooth) 3

3(4) A semicircular row of small teeth, the posterials (may be partly concealed by mucus) below the infraoral tooth bar, connecting the lower pair of lateral tooth plates; only two points on the centre pair of lateral tooth plates (Fig. 8B) .... Arctic lamprey, *Lampetra japonica* (Martens) .... (p. 51)



4(3) No posterials; two or three points on centre pair of lateral tooth plates; Pacific species not recorded so far from Bering Sea or Arctic Ocean drainages 5

5(6) Teeth sharp and strong; large median tooth on tongue; three points (rarely two) on centre lateral tooth plate on each side (Fig. 8C); vertical muscle grooves between last gill opening and vent, 65–70 (rarely 60–71) .... River lamprey, *Lampetra ayresi* (Gunther)

A Pacific coast parasitic species with known northern limit 15 miles north of Juneau, Alaska. Anadromous, predatory on fish, grows to 311 mm.

6(5) Teeth blunt; no distinct median tooth on tongue; usually two (rarely three) points on centre lateral tooth plate on each side (Fig. 8D); vertical muscle grooves between last gill opening and vent 60–77 ....Western brook lamprey, *Lampetra richardsoni* Vladykov and Follet

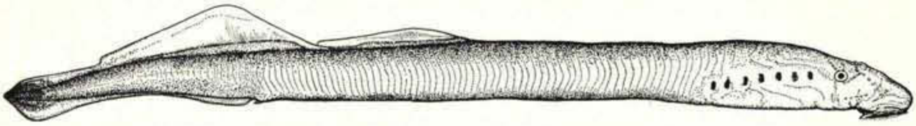
A Pacific coast nonparasitic species, perhaps extending north to Alaska. Formerly recorded as *Lampetra planeri,* its Eurasian counterpart. Fresh water only. Grows to 175 mm.

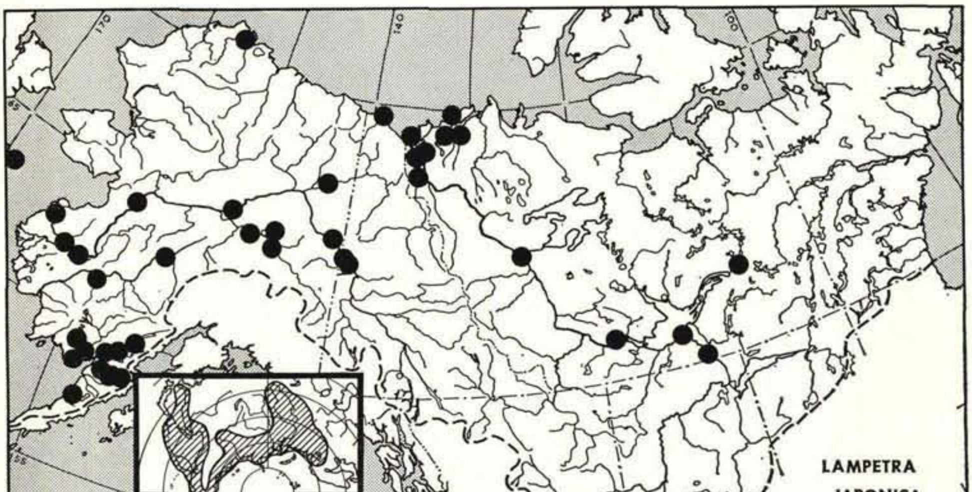
Fig. 8. Mouth cavities of lampreys:
(A) *Entosphenus tridentatus*
(B) *Lampetra japonica*
(C) *Lampetra ayresi*
(D) *Lampetra richardsoni*

Key to Young Lampreys (ammocoetes) in Our Area (no visible teeth, eyes rudimentary or absent, an oral hood partially encircling mouth, and fleshy papillae guarding the mouth aperture)

1(2) Lower half of oral hood pigmented (dark brown or blackish) .... Pacific lamprey, *Entosphenus tridentatus* (p. 57)

2(1) Lower half of oral hood unpigmented .... Arctic lamprey, *Lampetra japonica* (p. 51)




LAMPETRA
JAPONICA
MILES 400
KILOMETRES 600

ARCTIC LAMPREY

Lampetra japonica (Martens)

Lampetra means *a sucker of stone* and *japonica* means *of Japan*. The French common name for this species is *lamproie arctique.*

Distinguishing Characters

Any lamprey taken in the Yukon or Northwest Territories, or in Alaska north of Bristol Bay, is probably this species. In Bristol Bay drainages, the Arctic lamprey can be distinguished by tooth pattern (Fig. 8B) in adults, and colour pattern in ammocoetes.

Description

Body eel-like; head short, mouth surrounded by a circular sucking disk. Teeth sharp and strongly developed in the parasitic form; blunt and weakly developed in the smaller nonparasitic form. The typical tooth pattern is illustrated in Fig. 8B. Two or three pairs of bicuspid lateral tooth plates (rarely one or two plates are unicuspid); supraoral tooth bar usually with two teeth, very rarely also with a small median tooth; infraoral tooth bar with 5–10 teeth. A U-shaped row of small teeth (about 22), the posterials, connecting the lower lateral tooth plates below the infraoral tooth bar. Tongue with a large median point and about 6 or 7 smaller points on either side. Nostril single, median, and slightly anterior to eyes. Seven external gill openings. In adults, 5 or 6 velar tentacles at junction of oesophagus and respiratory tube (Fig. 9B). No paired fins; the two dorsal fin folds almost continuous in adults; caudal fin fold continuous with the posterior dorsal fin folds. No scales; in adults 65–80 muscle grooves between the last gill opening and the anus, 66–74 in ammocoetes.

Size: Adults of the parasitic form may grow to 62.5 cm (24.6 inches) long and ½ lb in weight (Berg, 1948–49), but are usually much smaller. Our largest Alaskan specimen is 41.1 cm. Adults of the nonparasitic form rarely exceed 18 cm (7.1 inches).

Sexual dimorphism: Mature males have a well-developed genital papilla, relatively high dorsal fin folds, and a very weakly developed ventral fin fold. In females the genital papilla is barely visible; the dorsal fin folds are lower than in males, and the ventral fin fold is well developed.

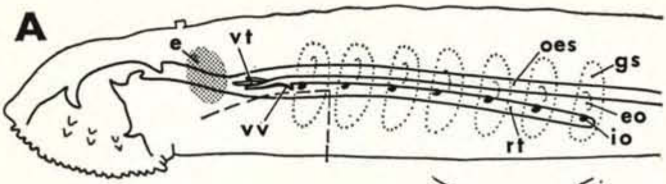


Fig. 9. Velar tentacles as a taxonomic character in lampreys. A, Diagrammatic lateral view; broken lines indicate cuts necessary to expose junction of respiratory tube and oesophagus. B, Ventral view of exposed velar tentacles, *Lampetra japonica.* C, Same view, *Entosphenus tridentatus.* *e* = eye; *eo* = external opening of gill sac; *gs* = gill sac; *io* = internal opening of gill sac; *oes* = oesophagus; *rt* = respiratory tube; *vt* = velar tentacle; *vv* = velar valve.

Colour: Adults fresh from the sea are dark blue above and silver below; in fresh water, adults are dark brown to blue–black above and light brown below. Ammocoetes are usually grey above and lighter below. The lower edges of the oral hood are about as dark as the dorsal head surface.

Distribution

In Eurasia, from Lapland (Pazreka River) eastward to Kamchatka, south to Korea. In Bering Sea, on St. Lawrence Island. On the North American mainland, from Kenai Peninsula, north along the Bering Sea drainages and east along Arctic Ocean drainages as far as Anderson River. Extending up the Yukon River into Yukon Territory, and up the Mackenzie River to Great Slave and Artillery lakes, and to Fort Smith on Slave River.

Taxonomic Notes

The taxonomic limits of the lamprey genera *Lampetra* and *Entosphenus* have been the subject of disagreement. Gill (1862) proposed the genus *Entosphenus,* with type *E. tridentatus,* but he did not give diagnostic characters for the genus. Jordan and Evermann (1896–1900) and Berg (1948–49) considered it to contain the single species *E. tridentatus,* and they diagnosed the genus as having three teeth on the supraoral tooth bar. According to this view members of the genus *Lampetra* may have the row of posterials or posterior labial teeth (the semicircular row connecting the lower pair of lateral tooth plates) either present or absent; *L. japonica* and *L. lamottei* are included.

On the other hand Regan (1911) considered this row of posterials (which are present in *E. tridentatus*) as the diagnostic feature of the genus *Entosphenus.* According to this view, followed by many including Hubbs and Lagler (1958), *Entosphenus* therefore includes, among other species, *japonicus* and *lamottei.*

A third more recent viewpoint is that because the posterials, considered by Regan as a key generic character, may be either present, incomplete, or absent within a single species (e.g. in some Japanese forms), therefore, there is no valid generic separation, and *Entosphenus* should be lumped with *Lampetra.*

Vladykov and Follett (1967) separate *Entosphenus* (apparently with only one named species, *E. tridentatus*) from *Lampetra*; their key would place *japonica* in the genus *Lethenteron.*

We believe that *Entosphenus tridentatus* stands apart from the other species discussed not only for reasons previously given, but also for the following. The velar tentacles, which in adults guard the junction of the oesophagus and the respiratory tube, consist in *E. tridentatus* of 11–16 fingers arranged as shown in Fig. 9C and described by Mather (1926). In contrast, all species of *Lampetra* examined had only seven or fewer velar tentacles, arranged in characteristic fashion with a median and one or two bifid lateral members (Fig. 9B). Furthermore, *E. tridentatus* has 50–63 fine points on each longitudinal lingual tooth plate, in contrast to 0–26 points in all *Lampetra* species examined. Accordingly the lumping of *Entosphenus* with *Lampetra* is unjustified.

Even without *E. tridentatus,* the genus *Lampetra* still contains a varied group of species. However, in view of our ignorance of their relationships, it seems best to avoid splitting up the genus *Lampetra* unless new information is forthcoming. Possibly the view of Vladykov and Follett (1967) that *japonica* belongs in the genus *Lethenteron* will be substantiated.

Another question concerns the relationship between the Arctic lamprey, *L. japonica*, and the American brook lamprey, *L. lamottei* (LeSueur), sometimes spelled *lamottenii.* The latter is an eastern North American form that is usually (but perhaps not invariably) nonparasitic, whose farthest northwestern range in western Ontario is separated by 1500 miles from the nearest *L. japonica* in Great Slave Lake. We have compared 40 Michigan and Ontario *L. lamottei* with 43 Alaskan and Mackenzie *L. japonica.* The ranges and mean numbers of velar tentacles and of teeth on the infraoral tooth bar are virtually identical in the two forms. Muscle groove counts are lower in eastern *L. lamottei* (64–76, mean 67.4) than in Mackenzie (68–74, mean 71.7, 7 specimens) or Alaskan (65–80, mean 69.4, 36 specimens) *L. japonica.* Further study may suggest that the two do not warrant specific separation. Presence or absence of a parasitic phase is no indication of specific differentiation, as the change from one life-history pattern to the other has apparently occurred several times within several different lamprey species. The American form was described as *Petromyzon lamotteni* by LeSueur in 1842, prior to naming of the Eurasian form as *Petromyzon japonicus* by Martens in 1868 (based on Japanese specimens). Because the name *lamottei* has priority, lumping *lamottei* and *japonica* would produce name changes in several wide-ranging Eurasian forms.

We believe that *L. lamottei* and *L. japonica* should be retained as separate species pending a review of all relevant species from both continents. An imaginative search for new taxonomic characters in lampreys might be fruitful.

Petromyzon borealis Girard from Great Slave Lake, and *Ammocoetes aureus* Bean from Yukon River, are synonyms of *Lampetra japonica.* In Siberia, the nonmigratory form has been recognized as a subspecies *Lampetra japonica kessleri,* but too little is known about variability in life histories of lampreys to usefully apply subspecific names at present.

Postglacial Dispersal

Arctic lampreys were probably present in the Bering region during Wisconsin glaciation, as well as farther west in Eurasia. Anadromous forms have probably moved east along the Arctic coast to invade successive river systems, and in some areas have developed nonmigratory populations such as those in the upper Yukon and in Great Slave Lake. The southeastern species *L. lamottei* probably survived glaciation south of the Great Lakes, and apparently has not since spread northward far enough to meet its northern counterpart.

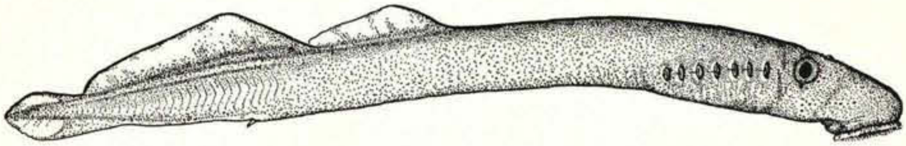
Biology

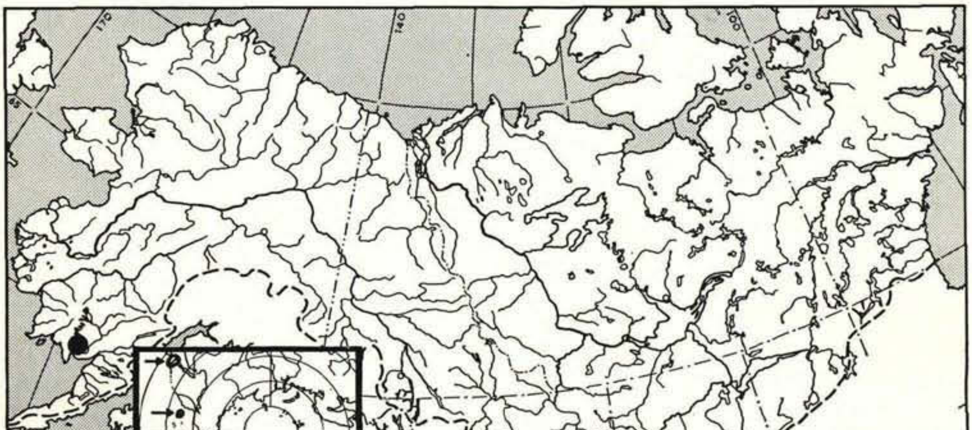
The life history of the Arctic lamprey is largely unknown, but it is obviously variable from place to place. Ammocoete larvae have been taken from muddy shallows along the whole length of the Yukon River, from the delta up to Dawson City, and from the Kuskokwim and several Bristol Bay drainages. After metamorphosis some of these migrate to sea and feed there by attaching to fish. Large lampreys ascend the lower Yukon in early spring, presumably on a spawning migration. We have adults up to 388 mm long taken in early June from the Tanana River, but whether they had migrated from the sea is unknown. Lampreys at least up to 254 mm long occur in Iliamna Lake and may be sea-run. Some definitely go to sea in Bristol Bay, for a transforming lamprey 122 mm and a small but sharp-toothed adult of 135 mm have been taken off Snag Point, Dillingham. In Nushagak Bay a lamprey 156 mm long was found attached to a chinook salmon, and a lamprey about 90 mm long with its head buried under the gill cover of a starry flounder was also found. Heard (1966) reports mature lampreys in the Naknek River system from 218 to 311 mm long that were probably anadromous. On the other hand some lampreys, supposedly of this species, apparently omit the migratory and possibly sometimes the parasitic phases in some Bristol Bay drainages. Adults, from 117 to 387 mm long, spawn in Brooks, Aleknagik, and other Bristol Bay watersheds between late May and mid-July; probably the larger ones have been feeding on fish, but perhaps not the smaller ones (although Heard (1966) failed to find metamorphosing ammocoetes with maturing gonads in the Naknek system, and thought that even the smallest mature lampreys he caught had probably been feeding parasitically). In Brooks Lake this species feeds on adult sockeye salmon and rainbow trout, and has been taken on juvenile salmon, pygmy whitefish, and even on a threespine stickleback. Our only specimens of this species from south of the Alaska Peninsula are small, perhaps non-parasitic, spawners (115–161 mm) from streams on the Kenai Peninsula. A non-migratory but parasitic population is reported to feed on whitefish in Tatlmain Lake tributary to Pelly River in Yukon Territory. A 411-mm specimen found dead on a St. Lawrence Island beach had undoubtedly been parasitic. Along the arctic coast at least some lampreys have a marine parasitic phase; a 355-mm specimen is recorded washed ashore at Point Barrow, and two smaller lampreys have been observed attached to fish (an inconnu and a smelt) in the sea at Herschel Island. Ammocoetes and an adult have been taken in the Mackenzie delta, and ammocoetes from the Anderson River. Upstream in the Mackenzie system, lampreys in Great Slave Lake are parasitic on whitefish, lake trout, and inconnu; these lampreys, although having a predatory stage, are rather small and probably never migrate to sea. A transforming ammocoete 170 mm long was collected from the Mackenzie River near Fort Providence.

Walters (1955) reports that lampreys probably spawn in Great Slave Lake and Artillery Lake in July. Heard (1966) describes spawning of *L. japonica* in the Naknek system, between May 28 and July 2, at water temperatures between 54 and 59 F. Nesting sites were shallow depressions in gravel-bottomed streams, in the main current at a depth of 8–20 cm of water. Both sexes participated in clearing the nesting site, picking up stones (and in one instance a small sculpin) with the oral sucker, and carrying them downstream. During spawning the male attached its oral sucker to the top of the female's head; their bodies were wrapped together, and vibrated rapidly while eggs and sperm were shed together. Berg (1948–49) reports that in the USSR large females may lay over 100,000 eggs. Ammocoetes bury themselves in the soft mud of stream margins and backwaters, their presence betrayed by a small hole on the mud surface. Ammocoetes have been found in stomachs of pike, and of herring gulls.

Some of the apparent variability in life histories may be because we are treating as a single species what are actually several species. Many more specimens are required from different places and at different stages.

Evermann and Goldsborough (1907a, b) report that Yukon River lampreys were at one time raked out by hooked sticks from under the ice by the thousands. Although now little used for food in North America, smoked lampreys probably of this species are attractively packaged and sold in Japan, and lampreys are of some commercial importance in Siberia. Ammocoetes may be used as bait.




ENTOSPHENUS
TRIDENTATUS
MILES
0
400
KILOMETRES
0
600
170
140
100

PACIFIC LAMPREY

Entosphenus tridentatus (Gairdner)

Entosphenus means *within wedge* (the tooth plate on the tongue being wedge-shaped) and *tridentatus* means *three-toothed,* referring to the supraoral teeth. The French common name for this species is *lamproie du Pacifique.*

Distinguishing Characters

Any large lamprey with three supraoral teeth (Fig. 8A) is probably this species. Ammocoetes of the Pacific lamprey can be distinguished by colour pattern.

Description

Body eel-like; head short; mouth surrounded by a circular sucking disk. Teeth sharp and strongly developed; the typical tooth pattern is illustrated in Fig. 8A. Four pairs of lateral tooth plates, the two middle pairs usually tricuspid and the other pairs bicuspid; supraoral tooth bar with sharp teeth at either end and a third tooth in the centre (very rarely absent), infraoral tooth bar usually with 5 teeth (occasionally 6 or 7). A semicircular row of small teeth (about 15–18), the posterials, the outer pair sometimes double, connecting the lower lateral tooth plates below the infraoral tooth bar. Tongue with a row of about 15–25 fine points, the median one scarcely larger than the others. Nostril single, median, and slightly anterior to eyes. Seven external gill openings. In adults 11–16 velar tentacles (Fig. 9C). No paired fins; the two dorsal fin folds almost continuous in adults; caudal fin fold continuous with the posterior dorsal fin fold. No scales; in adults 68–74 muscle grooves between the last gill opening and the anus; 64–70 in ammocoetes.

Size: Adults up to 760 mm (30 inches) in length and 1 lb in weight.

Sexual dimorphism: Mature males have a weakly developed genital papilla, relatively high dorsal folds, and no ventral fin fold; in females the genital papilla is barely visible, the dorsal fin folds are lower than in males, and the ventral fin fold is well developed.

Colour: Adults fresh from the sea are dark blue above and silver below; at spawning time adults are brownish red. Ammocoetes are grey above and lighter below; the lower edges of the oral hood are paler than the dorsal head surface.

Distribution

Pacific coast of North America from the Santa Ana River, southern California, to Unalaska; also recorded from near St. Matthew Island, and in the stomach of a whale off Bering Island near Kamchatka Peninsula. Okada (1960) reported it from the Yuhutu River, Hokkaido, Japan. Vladykov and Follett (1967) write that although this species is occasionally taken off Hokkaido, it is not definitely known to spawn in Japan. The Pacific lamprey is apparently rare north of the Alaska Peninsula; we have seen only one specimen from Wood River that enters Bristol Bay. Heard (1966) failed to find it during extensive collecting in Grosvenor Lake, despite an earlier report of the species there.

Taxonomic Notes

Reasons for retaining this species in a genus distinct from *Lampetra* are given in the "Taxonomic Notes" section of *Lampetra japonica.* It was described by Richardson in 1836 from the Willamette River as *Petromyzon tridentatus*, the description being attributed to a manuscript by Gairdner. Synonyms probably include *lividus, astori,* and *epihexadon,* none of which names have been used recently. Creaser and Hubbs (1922) recognize two subspecies *tridentatus* and *ciliatus* on the basis of adult myotome counts. If subspecies are recognized, the one in our area is *E. t. tridentatus.*

Postglacial Dispersal

The Pacific lamprey evidently survived south of glaciation on the Pacific coast of North America, and subsequently invaded successive river systems northwestward along the coasts of British Columbia and southeastern Alaska after ice withdrawal. The reported occurrence in northern Japan suggests the possibility of an additional Asian refuge, and its rare Bristol Bay occurrence indicates it might also have survived glaciation there.

Biology

Over most of its range, the Pacific lamprey migrates after metamorphosis to sea, where it feeds on fish and may grow to a large size. Newly metamorphosed individuals on their seaward migration have bright silver sides and dark blue backs, suggesting that they go through a process analogous to smolting in the salmons. Occasional nonmigratory and possibly nonparasitic races of Pacific lampreys have evolved, although less commonly than in the Arctic lamprey. Pacific lampreys in the

Cowichan River on Vancouver Island prey on fishes in fresh water and perhaps never migrate to sea. A small spawner (145 mm long) was taken from the Fraser River at Prince George, upstream of the range of large sea-run lampreys in the system, and lampreys of this species continue to spawn in parts of the Columbia River now cut off from marine migrants by impassable dams. Goose Lake in Oregon contains a landlocked dwarf race of *Entosphenus tridentatus* that may omit the predatory phase altogether.

Pacific lampreys spawn in riffles, where they excavate a shallow depression in the gravel, about 45 cm long.

Pacific lampreys up to 600 mm long spawn in the Copper River (Gulf of Alaska) in June. The only specimen we have examined from north of the Alaska Peninsula was taken from the Wood River near Aleknagik Lake (where *Lampetra japonica* also occurs).

THE STURGEONS — Family ACIPENSERIDAE

Sturgeons include the largest bony fishes in the world, some surpassing a ton in weight. They have a sharklike upturned tail, an extendable underslung mouth, four barbels under the snout, and rows of bony plates embedded in the skin (see sketch in Key to Families). Some enter the sea to feed, but all spawn in fresh water. None has been definitely recorded from our area, but there are several reports by natives and by explorers suggestive of sturgeons. A key is therefore provided to species known to approach our area. If a sturgeon is discovered and cannot be preserved, notes should be recorded of the various characteristics mentioned in the key, and if possible photographs or careful sketches kept.

KEY TO STURGEON SPECIES BORDERING OUR AREA

1(2) Lateral row of bony shields 23–30; centre of anal fin base lies opposite or behind posterior edge of dorsal fin base; gill rakers on first arch 18–20 .... Green sturgeon, *Acipenser medirostris* Ayres

A Pacific species found in Asia, in north Japan, Korea, and Sakhalin, and in North America from Los Angeles to southeastern Alaska, and from Unalaska. We have specimens from the Taku River, and Evermann and Goldsborough (1907a, b) report it from Copper River. Berg (1948–49) says "probably present also in the Bering Sea."

2(1) Lateral row of bony shields 30–56 (rarely 29); centre of anal fin base lies ahead of posterior edge of dorsal fin base; gill rakers on first arch 25–45 3

3(4) Barbels nearer to tip of snout than to mouth; dorsal row of bony shields usually 11 or 12 (rarely 13 or 14); gill rakers long and slender, more than three times as long as broad .... White sturgeon, *Acipenser transmontanus* Richardson

A Pacific species so far recorded from Monterey, California, to Cook Inlet, Alaska.

4(3) Barbels midway between tip of snout and mouth, or closer to mouth; dorsal row of bony shields usually about 15 (rarely 9–19); gill rakers not over three times as long as broad, may be fan shaped .. 5

5(6) Lateral row of bony shields usually about 36 (range 29–42); dorsal fin rays about 35; tips of pelvic fins usually do not reach behind front of dorsal fin base .... Lake sturgeon, *Acipenser fulvescens* Rafinesque

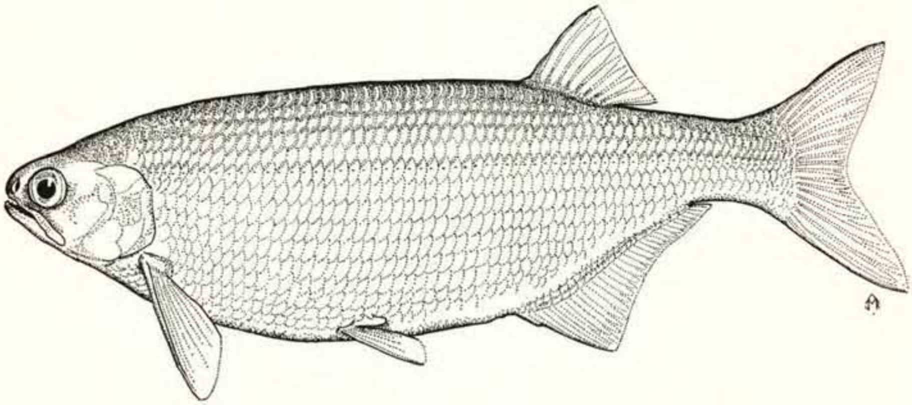
Ranges from the Saskatchewan River in Alberta eastward to the lower St. Lawrence River, and south to Alabama. Extends north on the west side of Hudson Bay to Seal River just north of Churchill, Manitoba.

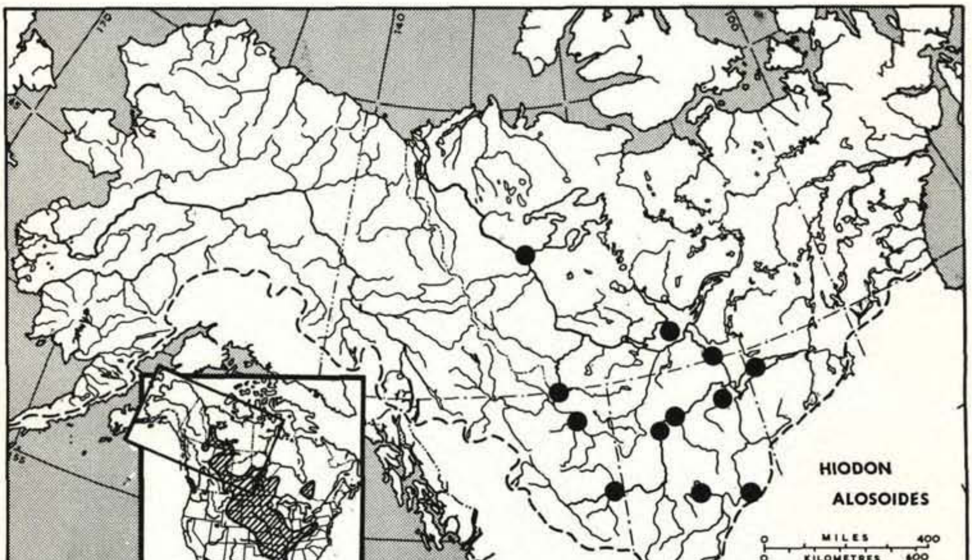
6(5) Lateral row of bony shields usually over 41 (range 37–56); dorsal fin rays usually 43–46 (rarely 38–52); tips of pelvic fins usually reach behind front of dorsal fin base .... Siberian sturgeon, *Acipenser baeri* Brandt

A species found in rivers of the USSR draining into the Arctic Ocean, from the Pechora eastward to the Kolyma rivers. Enters the arctic seas. Walters (1955) suggests it may occur in arctic Alaska.

THE MOONEYES — Family HIODONTIDAE

The mooneyes are primitive fishes superficially resembling herrings. They are deep-bodied and silvery, with blunt snouts, many teeth, numerous anal fin rays, and no adipose fin. There are probably only two species of mooneyes, both confined to fresh water of North America, one occurring in our area.





HIODON
ALOSOIDES
0 MILES 400
0 KILOMETRES 600

GOLDEYE

Hiodon alosoides (Rafinesque)

Hiodon means *hyoid tooth* (the Y-shaped basihyoid bone forming the base of the tongue bears teeth) and *alosoides* means *shadlike*. The French common name for this species is *laquaiche aux yeux d'or*.

Distinguishing Characters

The long anal fin and placement of dorsal fin far back characterizes this species.

Description

Body deep, compressed; head short, more than four times into total body length; eye large, equal to or greater than snout, snout short and blunt. Mouth oblique, terminal, with well-developed teeth in both jaws and on tongue, basibranchials, palatines, pterygoids, and parasphenoid. Branchiostegals 7–10 + 7–10; gill rakers short 6–7 + 10–11. Dorsal fin originates behind origin of anal fin; 9 or 10 major dorsal rays; 29–35 major anal rays; 11 or 12 pectoral rays and 7 pelvic rays. Scales large, cycloid, 58–62 pored scales in lateral line. Vertebrae, 58–61. One pyloric caecum. Gasbladder large, with an auditory extension through an opening in the lateral wall of each otic capsule in the skull.

Size: Length to 508 mm (20 inches) and weight to about 1.4 kg (3 lb 2 oz).

Sexual dimorphism: In mature males the anterior rays of the anal fin are somewhat elongate, forming a distinct lobe that is absent in females and juveniles.

Colour: In adults the sides are silvery and the back bluish. The iris of the eye is bright golden. In small specimens (less than 6 inches) the sides are a pale brown, and the back a somewhat darker brown; the iris of the eye is silvery.

Distribution

In the Mississippi River and tributaries from Louisiana north, and in the rivers of the Great Plains from the Missouri to the Mackenzie systems. In the Churchill, Nelson, and Severn river systems, Lake Abitibi, and the Nottawa River system, including lakes Matagami and Waswinipi, in Quebec, but absent from the St. Lawrence River basin except for Lake Temiskaming on the Ottawa River. In the Mackenzie River downstream as far as Great Slave Lake, and in the Liard River in British Columbia; a single fish is also recorded from Fort Norman (Preble, 1908). Details of distribution limits are given by Kennedy and Sprules (1967).

Taxonomic Notes

The goldeye was named as *Amphiodon alosoides* (misprinted *alveoides*) by Rafinesque in 1819. Since then some authors have used this name, whereas others have placed both the goldeye and its relative the mooneye, *Hiodon tergisus*, in one genus, *Hiodon* (sometimes with the spelling *Hyodon*). Differences between the two species are primarily in position of the dorsal fin, extent of keeling on the belly, fin ray counts, and eye colour. Because the family contains only two species, which do not differ strikingly, we follow Cavender (1966) in using a single generic name to indicate their close relationship. Richardson's *Hyodon chrysopsis* (1836) from Cumberland House on the lower Saskatchewan River was apparently this species.

Postglacial Dispersal

Goldeyes have a unique pattern of distribution, occupying a band in the centre of the continent reaching from the lower Mississippi to the lower Mackenzie River; they also are present in some Hudson Bay tributaries north of the Great Lakes and as far east as Quebec, and yet they are absent from all the Great Lakes. Metcalfe (1966) suggests that they originally inhabited the preglacial northward-flowing Missouri River (described under "Outline of Geological History").

Probably goldeyes survived Wisconsin glaciation in the Missouri River (but not the upper Mississippi, from which they are currently absent). They probably moved into Lake Agassiz, whose area, described under "Outline of Geological History," at one time included Sandy and Finger lakes on the Severn River in northwestern Ontario that now contain goldeyes (Ryder et al., 1964). During the late stages of Lake Agassiz, glacial Lake Barlow-Ojibway lay north of the present height of land separating the Great Lakes and Hudson Bay drainages, and Agassiz and Barlow-Ojibway were probably joined (Elson, 1967). Goldeyes probably moved eastward into Barlow-Ojibway from Agassiz at this time, and thereby came to occupy the present Lake Abitibi and the Nottaway River basin, which lie in the old Barlow-Ojibway lake basin. Lake Temiskaming also lay in this basin, although it now empties south into the St. Lawrence system.

Their entrance to Lake Agassiz may have been late (Gimli phase of Elson (1967)), after the last connection to Lake Superior had closed. If, as might be expected, they had entered Lake Agassiz earlier, it is difficult to understand their absence from the Great Lakes. Their absence from the upper Mississippi during deglaciation also requires explanation, in that the northwestern tributaries of upper

Missouri River (their supposed refuge) and the upper Mississippi River were linked farther south. Perhaps silted waters to which the goldeye is adapted characterized the western refuge, whereas in the east the vast settling basins of proglacial lakes discharged clear and hence unsuitable water into the present upper Mississippi River valley. Alternatively, waterfalls on the Mississippi River may have blocked ascent of fish during some of the period discussed.

Biology

The goldeye frequents large muddy rivers, and tolerates very turbid water. It is sometimes found in quite swift current. In lakes it prefers turbid shallows; in Lake Athabasca goldeyes are numerous in the shallow waters of the west end, especially in the river channels and flat expanses near the delta (Rawson, 1947b). Goldeyes apparently feed largely in surface waters, in Lake Athabasca and Great Slave Lake, taking mostly aquatic and terrestrial insects; larger goldeyes may eat small fish such as trout-perch, sticklebacks, and young pike, and also mice. Molluscs have been found in goldeye stomachs. Feeding probably occurs principally at night. The peculiarities of the eye may be adaptations for nocturnal vision (and for vision in turbid water). The retina in most vertebrate eyes contains a mixture of rod-shaped and cone-shaped sensory elements. Rods predominate in the eyes of some nocturnal predators, such as owls, that can see in very dim light, and cones predominate in animals such as eagles that can distinguish very fine details under bright illumination. Goldeyes have exclusively rod elements in their large eyes (Moore and McDougal, 1949). Perhaps in the process of acquiring the ability to see under very low light intensity they have sacrificed the ability to distinguish colours, for colour vision seems to be linked with cone elements of the retina. Lack of colour vision would be no handicap with respect to courtship or mating in goldeyes, for the sexes show no distinctive breeding colours.

Goldeyes grow rapidly in their first few months of life; in Lake Claire, Alberta, the average fork length of goldeye yearlings was 69 mm (2.7 inches) and 91 mm (3.6 inches) in samples collected in different years (Battle and Sprules, 1960). Most of the commercially caught Lake Athabasca goldeyes ranged from 6 to 11 years old, with lengths from 304 to 418 mm (12–16.5 inches) and weights from 0.3 to 0.9 kg (11 oz to 2 lb) (Rawson, 1947a–c). Growth is slightly slower than this in Great Slave Lake, and faster in Manitoba lakes. Among older fish, females grow faster than males (Kennedy and Sprules, 1967).

Males reach sexual maturity one year earlier than females; in Lake Claire males mature at ages from 6 to 9 and females from 7 to 10 (Battle and Sprules, 1960). In southern Manitoba maturity is advanced 2 or 3 years. Adult females probably spawn each year once they are mature (Kennedy and Sprules, 1967).

In northern waters goldeye begin to spawn in spring shortly after the disappearance of ice cover, usually starting in late May and extending to the first week of July. Fish ascend rivers or tributary streams, and spawn on gravel shoals or in quiet expansions, perhaps during hours of darkness. In the North Saskatchewan River they continue upriver after spawning, some feeding in the vicinity of Edmonton in autumn (Paterson, 1966). Large females may lay over 25,000 eggs. The fertilized eggs are about 4 mm in diameter, with a wide space between the spherical semi-transparent egg capsule and the cream-coloured yolk. A large oil globule is present. The capsule is apparently nonadhesive, and the egg is unusual among North American freshwater fishes in that it is semibuoyant. Larvae hatch at a length of about 7 mm. At hatching the large oil globule occupies an extensive portion of the yolk sac immediately behind the heart; the larvae float at first at the water surface in a vertical position buoyed up by the oil droplet.

Goldeyes are not usually marketed fresh, but when smoked and dyed "Winnipeg goldeye" is one of the finest of all eating fish. The fish, which are always frozen, are thawed, dressed, soaked in brine, artificially stained to produce an attractive golden orange colour, and then treated for several hours in the hot smoke of oak logs. "A 'Winnipeg goldeye' represents the triumph of art over nature. Its characteristic colour results from an aniline dye. Its characteristic taste is essentially that of oak wood smoke. Its texture has been improved by freezing. Its name is derived from a lake where it is no longer caught in appreciable quantities." (Kennedy and Sprules, 1967). The demand for this delicacy exceeds the supply. Commercial gillnet fisheries exist in Lake Claire west of Lake Athabasca, and in Manitoba and in Sandy Lake, Ontario. The only significant commercial fishery for goldeye in the United States is in Red Lake, Minnesota. About 283,000 lb were produced in 1960, but annual production since then has averaged less than 200,000 lb. Symington (1959) warns: "Smoked and dyed cisco have been passed off for goldeye, but the flavour is not comparable. Since it is customary to serve the goldeye with head intact, the diner needs only to follow the maxim of the horse-trader and look the creature in the mouth to make sure he's getting value for his money. If there are teeth, the fish is probably a genuine goldeye; if there are no teeth and the flesh is dryer and less flavourful, he's probably eating cisco and paying for goldeye."

In streams, the goldeye is a very game and vigorous fish, which rises to the dry fly after the manner of a trout. It is also caught by anglers on a baited hook or small spinner.

Another curious feature of this unusual fish is that the retina of the eye reflects light as does that of a cat. Bajkov (1930) writes (rather breathlessly): "The author was astonished when, during a dark night, he was lifting gill nets containing this fish by flashlight, the eyes were so bright and fluorescent that it is almost impossible to describe this remarkable phenomenon."

THE WHITEFISHES — Family COREGONIDAE

Whitefishes are related to the salmonids (trout, char, and salmon) and the graylings, which also possess a single soft dorsal fin plus an adipose fin, and have a scaly process at the base of each pelvic fin. Whitefishes, however, do not have strong teeth in the jaws, and their scales are rather large. Some grow to a large size, and many are commercially important in the north as human and dog food. They inhabit both lakes and rivers, and a few venture into the sea. As far as is known all northern species spawn in autumn or winter, shedding small pale eggs over gravel or rocks without preparation of nest or "redd."

Whitefishes are widespread in cooler parts of the northern hemisphere. Dozens of different species have been described, but their relationships are poorly understood. During each glaciation whitefish populations were isolated in various meltwater lakes around the margins of the ice, some in the north and some the south. Sometimes isolation was protracted enough for the evolution of separate species in separate areas, so that when new water connections formed during withdrawal of the ice the two kinds of whitefish might invade each other's areas without interbreeding. In other instances where divergence had not proceeded quite so far the removal of ice barriers resulted in two slightly different kinds of whitefish hybridizing when their ranges rejoined. The characters of whitefish are highly subject to modification by the conditions under which the young develop, so that the same species may appear quite different in different lakes. To further complicate their taxonomy, the same species may occur in North America, USSR, and Europe, and may have been given different names in different countries. Hence, the species names and descriptions that follow are only tentative, partly because much more information is required, and partly because whitefishes do not always fall into categories that conform to our formal system of naming species. In the following key three of the most difficult groups are identified only as *"Coregonus clupeaformis"* complex, *"Coregonus artedii"* complex, and *"Coregonus sardinella"* complex. For discussion of the possible species in each of these complexes, the reader is referred to the appropriate taxonomic notes.

The major groupings of whitefishes are more clear-cut. Three genera are recognized. The inconnu is the only species in the genus *Stenodus*; it is primarily a fish-eater, and possesses a large pikelike mouth with fine teeth. The remaining species fall either into the genus *Prosopium* or the genus *Coregonus*. Species of *Prosopium* tend to have rounded bodies, their young have dark parr marks, and they share single nostril flaps and various distinctive osteological features. Species of *Coregonus* are more often deep-bodied, their young are an unmarked silver, and they have double skin flaps between the nostrils. All species of *Prosopium* have a bone in the floor of the mouth (the basibranchial plate) that is absent in all *Coregonus* (Norden, 1961).

Some species of *Coregonus* have developed as midwater plankton feeders with large mouths, protruding lower jaws, and many fine gill rakers. These "ciscoes" or "freshwater herrings" used to be placed in a separate genus *Leucichthys* (or *Argyrosomus*), but the characters have probably evolved independently more than once under common selective pressures; they intergrade in degree between different species and within single species in different lakes and at different sizes. Even the genus *Prosopium* has produced ciscolike species in the western United States. Hence these characters do not indicate common ancestry, and should not be taken as characterizing a distinct genus.

KEY TO THE SPECIES

1(10) Lower jaw projects beyond, or is equal to, upper jaw; profile of upper lip slopes backwards in line with the forehead (Fig. 10A) 2

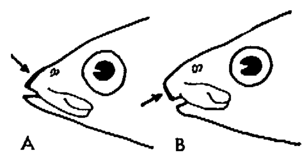


Fig. 10. A, Head of a cisco; B, head of lake whitefish.

2(3) Mouth large, maxilla extends to the posterior margin of the pupil; 13–17 gill rakers on the lower limb of 1st gill arch .... Inconnu, *Stenodus leucichthys nelma* (Pallas) (p. 75)

3(2) Mouth moderate, maxilla does not extend to the posterior margin of the pupil; 21–35 gill rakers on lower limb of first gill arch (Fig. 11) 4

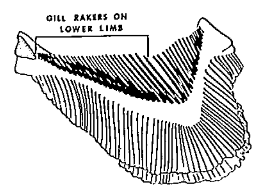


Fig. 11. First left gill arch of *Coregonus autumnalis.*

4(7) Tip of lower jaw projects slightly beyond tip of upper when mouth closed; pelvic fins often black-tipped or dusky 5

5(6) Pelvic fins inserted far back, the distance from snout to front of pelvic base equals the distance from front of pelvic base to a point on the caudal fin rays posterior to the caudal flexure (Fig. 12A) .... Lake cisco, *"Coregonus artedii"* .... complex (p. 91)

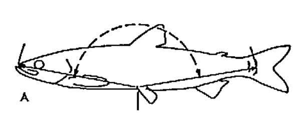
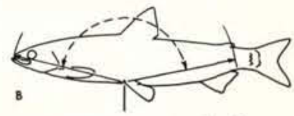


Fig. 12. Relative positions of pelvic fins. A, *Coregonus artedii;*

6(5) Pelvic fins inserted forward, the distance from snout to front of pelvic base equals distance from front of pelvic base to a point on the peduncle ahead of the caudal flexure (Fig. 12B) .... Least cisco, "*Coregonus sardinella*" .... complex (p. 97)



B. *Coregonus sardinella.*

7(4) Tip of lower jaw does not project beyond upper jaw when mouth closed; pelvic fins never black tipped or dusky 8

8(9) 21–25 gill rakers on lower limb of first gill arch .... Bering cisco, *Coregonus laurettae* Bean (p. 107)

9(8) 26–31 gill rakers on lower limb of first gill arch (Fig. 11) .... Arctic cisco, *Coregonus autumnalis* (Pallas) (p. 103)

10(1) Snout projects well beyond tip of lower jaw; profile of upper lip vertical or overhanging (Fig. 10B) 11

11(16) Transparent membrane surrounding eye with a distinct notch below hind margin of pupil (Fig. 13); single flap between nostrils (Fig. 14A) 12

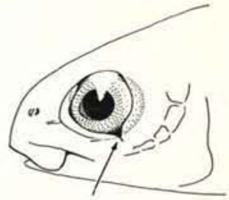


Fig. 13. Head of *Prosopium cylindraceum*, showing notch in adipose eyelid.

12(13) Snout blunt; 50–70 pored scales in lateral line; 14–33 pyloric caeca .... Pygmy whitefish, *Prosopium coulteri* ...... (Eigenmann and Eigenmann) (p. 119)

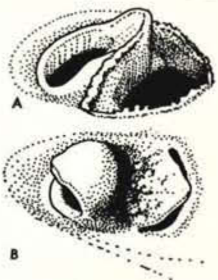


Fig. 14. A, Nostril with single flap (*Prosopium*). B, nostril with double flap (*Coregonus*).

13(12) Snout pointed; 72–104 pored scales in lateral line; 50–130 pyloric caeca 14

14(15) 20–23 (rarely 24) scale rows around the caudal peduncle (Fig. 15); 13–18 gill rakers on the lower limb of first gill arch .... Mountain whitefish, *Prosopium williamsoni* .... (Girard) (p. 115)

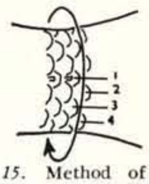


Fig. 15. Method of counting numbers of horizontal scale rows crossing narrowest part of caudal peduncle.

15(14) 24–27 scale rows around the caudal peduncle; 9–13 gill rakers on the lower limb of first gill arch .... Round whitefish, *Prosopium cylindraceum* (Pallas) (p. 111)

16(11) Transparent membrane surrounding eye without a distinct notch below pupil; double flap between nostrils (Fig. 14B) 17

17(18) Brow rounded in profile (Fig. 16A), no hump in adults; length of longest gill raker less than one-fifth interorbital width (Fig. 17A) .... Broad whitefish, *Coregonus nasus* .... (Pallas) (p. 87)

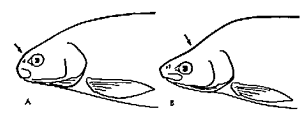


Fig. 16. A, Convex brow of *Coregonus nasus;* B, concave head profile of *Coregonus clupeaformis.*

18(17) Brow concave in profile (Fig. 16B), adults usually with a hump behind the head; length of longest gill raker more than one-fifth interorbital width (Fig. 17B) .... Humpback ...... whitefish, *"Coregonus clupeaformis"* ...... complex (p. 79) — Barren Grounds, Mackenzie system, and upper Yukon system; modal gill-raker counts 26 or more .... *Coregonus clupeaformis* (Mitchill) .... (p. 79) (occurs sympatrically in the upper Yukon system with *C. pidschian*)

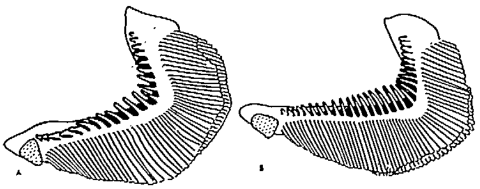
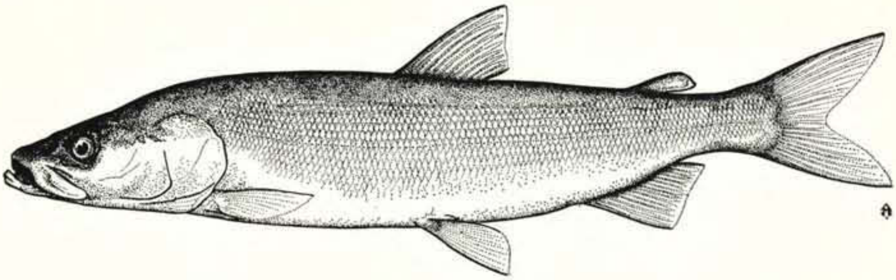
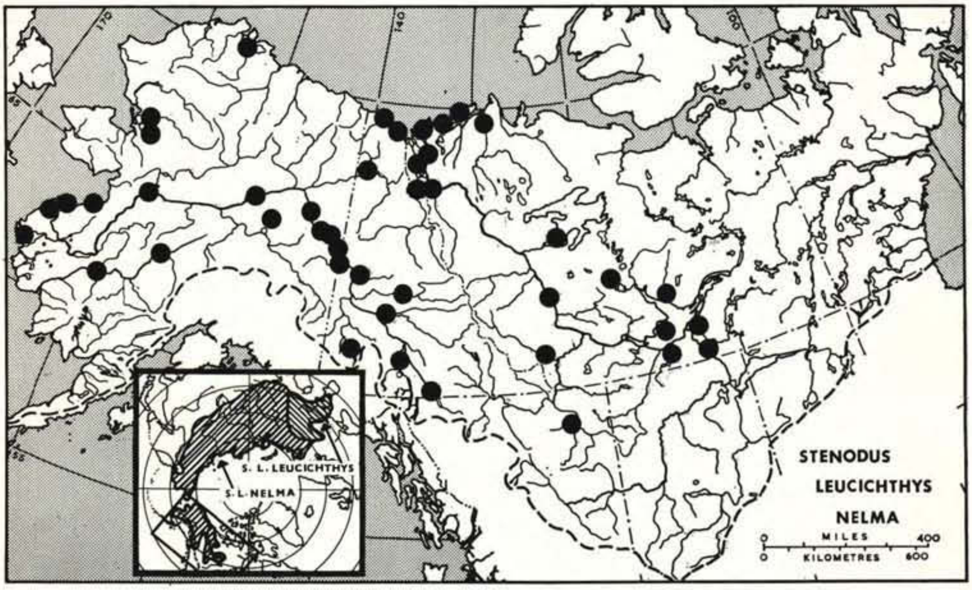


Fig. 17. First left gill arch: A, *Coregonus nasus;* B, *Coregonus clupeaformis.*

18(17) — Central Yukon system and lower Mackenzie region; modal gill-raker counts 24 or 25 .... *Coregonus nelsoni* (Bean) (p. 79)

— Lower Yukon system, Bering Sea regions, and isolated populations in the upper Yukon system; modal gill-raker counts 21, 22, or 23 .... *Coregonus pidschian* (Gmelin) (p. 79)




170
140
100
65
155
S. L. LEUCICHTHYS
S. L. NELMA
STENODUS
LEUCICHTHYS
NELMA
0 MILES 400
0 KILOMETRES 600

INCONNU

Stenodus leucichthys nelma (Pallas)

Stenodus means *narrow tooth*; *leucichthys* means *white fish*; and *nelma* is the Russian name for this fish. The French common name for this species is *inconnu.*

Distinguishing Characters

This species is a long silvery fish with large, wide mouth extending back to the posterior edge of the pupil and a projecting jaw.

Description

Body elongate, pikelike, compressed; head long, usually less than four times into standard length; eye moderate, less than one-quarter head length; snout about one-quarter head length. Adipose eyelid without a ventral notch. Mouth large, lower jaw projecting beyond the upper, with very small teeth (some in bands) on the anterior portion of the lower jaw, the premaxillae, head of maxillae, tongue, head of vomer, and palatines; no basibranchial teeth. Double flap between the nostril openings. Branchiostegals 9–12 + 9–12; gill rakers moderate 6–9 + 12–18 (total 19–24 in North America, 18–26 in USSR). Dorsal fin with 12–19 major rays; 15–18 major anal rays; 16 or 17 pectoral rays; and 11 pelvic rays. Scales large, cycloid, 90–110 pored scales in lateral line in North America (88–121 in USSR). Vertebrae 64–69. Pyloric caeca 150–202 in our area (99–239 elsewhere).

Size: Total length in North America 150 cm (59.2 inches) and weight 28.5 kg (63 lb); usually much smaller. Said to reach 40 kg (88 lb) in Siberia.

Sexual dimorphism: There are no obvious external differences between the sexes.

Colour: Dark green to light brown above, and silver below. Dorsal fin usually dusky; the other fins immaculate. Dorsal part of the head and tip of lower jaw dark. Young coloured like the adults and without parr marks.

Distribution

This subspecies ranges in Eurasian arctic watersheds from the White Sea to Bering Strait, and south to northern Kamchatka. In North America, south on Bering Sea drainages to the Kuskokwim River, and east on Arctic Ocean drainages to Anderson River. Ascending the Yukon River to its headwaters in Teslin Lake, B.C., and the Mackenzie River as far as Fort Nelson on the Liard system and the rapids at Fort Smith on Slave River. Entering brackish and salt water. The subspecies *S. l. leucichthys* occurs in the northern Caspian Sea and its tributaries.

Taxonomic Notes

The inconnu was first described as *Salmo leucichthys* from Caspian Sea drainages by Güldenstadt in 1772. *Salmo nelma* was described from rivers of Siberia by Pallas in 1776; Richardson described *Salmo mackenzii* from the Mackenzie River basin in 1823. Later studies showed all the North American and Asiatic fish to belong to the same species. North American inconnu have since been referred to as *Stenodus leucichthys mackenzii*; we follow Shaposhnikova (1967) who demonstrated that the Siberian and North American fish form one subspecies *S. l. nelma* (Pallas), from which the Caspian fish *S. l. leucichthys* (Güldenstadt) differ in osteology of the head.

Postglacial Dispersal

The range of the inconnu is much wider in Eurasia than in North America. Its absence east of Anderson River suggests that it may have moved eastward only in comparatively recent times from the Bering area or arctic Siberia.

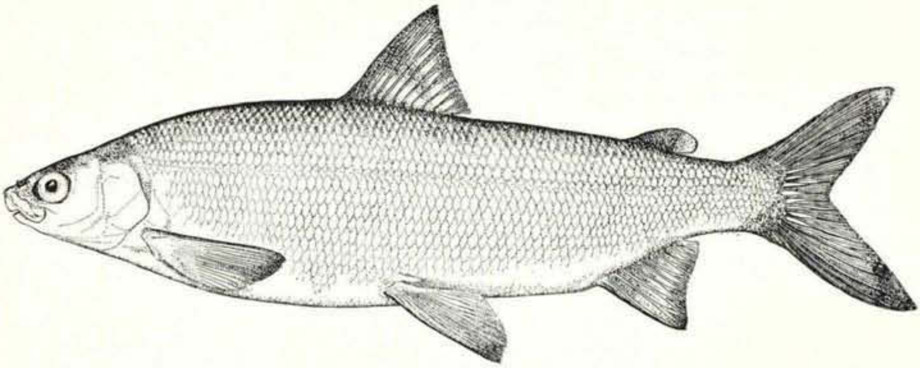
Biology

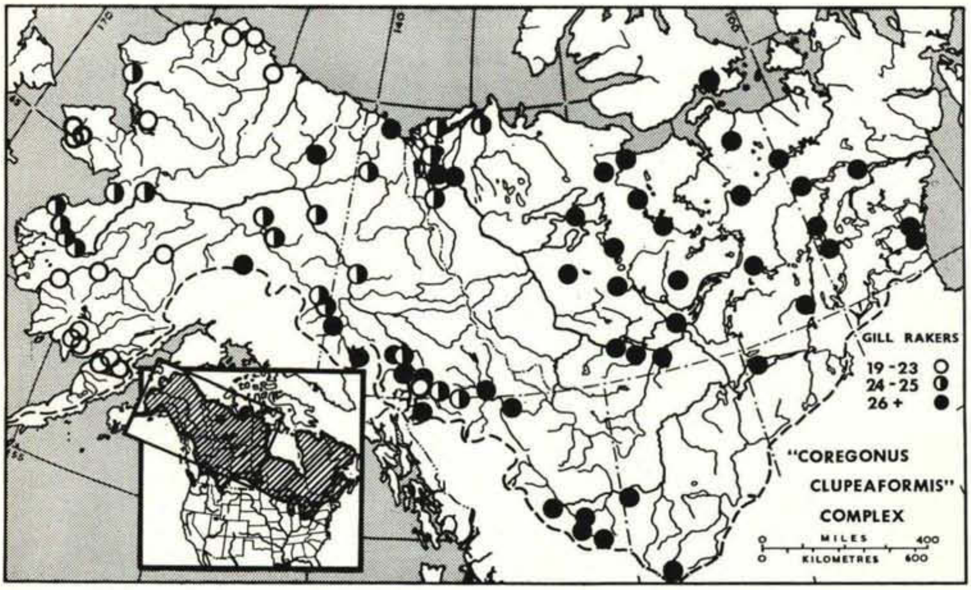
Inconnu are most abundant in the large, muddy northern rivers and in associated lakes. Adult inconnu are voracious and feed mainly on small fishes (particularly young whitefish, minnows, sticklebacks, and lamprey ammocoetes, and, in the upper Yukon River, on young chinook salmon), whereas the young feed primarily on aquatic insects and crustaceans. Inconnu are not usually cannibalistic, but Larkin (MS cited in Fuller, 1955) observed that mature inconnu at the mouth of Big Buffalo River, N.W.T., were gorged with young inconnu. In the lower Mackenzie, Kobuk, Yukon, and Kuskokwim rivers the inconnu are anadromous, but probably do not stray far from the mouths of these large rivers. The inconnu in Teslin and Great Slave Lake are apparently not anadromous, but those in Great Slave Lake do migrate up large tributary rivers in the late summer. This upstream migration is not obvious and may take place over several summer months. In contrast, the post-spawning downstream migration is rapid and spectacular. A "tremendous rush" of spawned-out adults descends the larger tributary streams of Great Slave Lake (Big Buffalo, Little Buffalo, Slave, Taltson, and Hay rivers) at a definite period each autumn. These downstream migrations are well known to the natives of the area, and the main fishery on inconnu occurs at this time. Presumably, spawning occurs in these same rivers in late summer and early fall (probably just before the downstream migration). According to Berg (1948–49), females lay from 130,000 to 420,000 eggs. Probably no nest is built, and the eggs are simply scattered over gravel in riffle areas. However, no one (to our knowledge) has recorded the spawning behaviour of the inconnu. In Big Buffalo River the young probably remain for 2 years before entering Great Slave Lake. In Great Slave Lake, inconnu mature in 7–10 years and live up to 11 years (Fuller, 1955), but in parts of Siberia they do not mature until up to 18 years old and apparently live as long as 21 years (Berg, 1948–49).

This species is variously fished throughout the north by gillnet, angling, or fish wheel, particularly in autumn and winter. The commercial catch of inconnu in Great Slave Lake in 1963 was 344,000 lb, and in the Kotzebue–Selawik area of Alaska a small commercial fishery supplies up to 100,000 lb of inconnu annually for the local market (Alt, 1965). Much of this fish is dried and used for dog food. Inconnu are also sought by sport fishermen using a troll or minnow, particularly on the Yukon River. They are described as hard fighters when taken thus. In contrast, inconnu caught in gillnets are almost always placid or dead, perhaps because their tapering heads are inserted in the net mesh so as to constrict their breathing.

The quality of the inconnu as a food for humans is apparently a matter of taste. Richardson (1836a, b) wrote "Its flesh is white, and when in good condition, tolerably palatable, though rather soft and oily, and soon becoming disagreeable when used as daily food," whereas Mr K. H. Lang (as quoted by Dymond, 1943) states that "a piece of the tail of a big connie is generally considered the best feed of fish obtainable in the country." The rich flavour and high oil content suggest that inconnu may prove suitable for smoking, mild curing, or canning.

The French name *poisson inconnu* ("unknown fish") was applied to this fish by Sir John Richardson's voyageurs who had not encountered it in more southerly waters. "Inconnu" has been corrupted to "cony" in parts of the north. Another common name is "sheefish"; Samuel Hearne took this fish in Great Slave Lake in January 1772, and records that "the Northern Indians call this fish Shees."




GILL RAKERS
19 - 23
24 - 25
26 +
"COREGONUS
CLUPEAFORMIS"
COMPLEX
MILES
400
KILOMETRES
600

HUMPBACK WHITEFISH

"Coregonus clupeaformis" complex including *Coregonus clupeaformis* (Mitchill) *Coregonus pidschian* (Gmelin) and *Coregonus nelsoni* (Bean)

Coregonus means *pupil of eye (in) angle (of head)*; *clupeaformis* means *herring-shaped*; *pidschian* is the common name for this whitefish in the Ob region of Siberia; and *nelsoni* is derived from E. W. Nelson, ornithologist, who collected the first specimens in Alaska. The French common name for this species is *grand corégone*.

Distinguishing Characters

Tip of snout projecting beyond tip of lower jaw; body flat-sided, not round in cross section; brow concave in profile; gill rakers longer than one-fifth the space between the eyes.

Description

Body compressed, the sides somewhat flattened particularly in large fish; head short, usually more than four times into standard length. Large fish may develop a distinct hump behind the head, producing a concave dorsal profile (Fig. 16B). This hump is perhaps higher and more sharp-edged in Alaskan than in Barren Grounds fish. Adipose eyelid without a ventral notch. Snout projects beyond tip of lower jaw; profile of upper jaw vertical, or more often sloping down and back. Length of snout and mouth variable, the maxilla usually but not invariably reaching behind the anterior edge of the eye; maxilla length 22–28% of head length; maxilla length 2.2–2.9 times maxilla width; maxilla length more than three-quarters of interorbital width in fish of 25 cm standard length (about 11 inches fork length) or larger; in smaller fish, maxilla length more than four-fifths of interorbital. Teeth not evident in jaws or in mouth. Double flap between the nostril openings. Branchiostegal rays 8–10 on either side. Total gill-raker counts in our area 19–33 (7–12 + 12–21), with mean counts generally lower towards the west; length of longest gill raker 1.32–1.97% of standard length, or 22–44% of interorbital width (Fig. 17B). Dorsal fin with 11–13 major rays; anal fin with 10–14 major rays; about 15–17 pectoral rays; and about 11–12 pelvic rays. Scales large, cycloid, 77–95 pored scales in lateral line, 8 or 9 in suprapelvic row, 22–29 scale rows around caudal peduncle. Vertebrae 59–64 in our area (56–64 over whole range). Pyloric caeca 140–222.

Size: Total weight 10 kg (22 lb) in our area; a 42-lb fish was reported from Lake Superior in about 1918. A 4.9-kg specimen (10.7-lb) was 73 cm (28.8 inches) long.

Sexual dimorphism: Males at spawning time may develop hard white conical tubercles on the scales (particularly along the sides) and scattered on the head. Tubercles are poorly developed or absent in females.

Colour: Back dark brownish or greenish, belly silver or yellowish. The overall appearance may be silvery, or, in some waters, the fish may be dark brown, with patterns of dark outlining the scale rows. Fins may be pale or dusky, but without patterned markings. Young are silvery, without parr marks.

Distribution

Across the northern North American mainland from Bering Strait to Labrador. On the Pacific slope in the Susitna, Copper, Alsek, Skeena, and upper Fraser river systems. Hudson Bay, Great Lakes, and St. Lawrence River drainages, and south to Hudson River and the Susquehanna River system. Introduced in cool lakes outside of its natural range.

In our area, generally distributed throughout mainland drainages, and on Victoria Island; sometimes taken in the sea.

Coregonus pidschian, which is probably part of this complex, extends eastward across arctic Siberia at least as far as the Ob River and perhaps into Europe.

Taxonomic Notes

Amongst those North American members of the genus *Coregonus* that are not ciscoes (i.e., those that have fewer than 33 gill rakers and have the snout overhanging the tip of the lower jaw), there is on the one hand the broad whitefish *C. nasus* (with short gill rakers and wide head), and on the other hand a group of humpback whitefishes treated here collectively as *"Coregonus clupeaformis"* complex.

The best character now in general use for separating species within this complex seems to be gill-raker number. Svardson (1957) has stated that gill-raker count, unlike most other morphological characters, is largely determined genetically, and can therefore indicate hereditary relationships between fish reared in different environments. Unfortunately, even gill-raker numbers are subject to slight environmental modification, and also can probably be altered over a few generations by selective pressures. Environmental alteration of gill-raker count has been demonstrated in 30 *C. clupeaformis* reared all their lives in captivity, whose modal raker count was less than their parental Lake Erie stock (Koelz, 1929). (Svardson (1965) suggests that there may have been unintentional selection of some extreme parent fish in this experiment; however, the lowest counts in the captive fish were lower than those of any of hundreds of wild fish reported by Koelz (1929) not only from Lake Erie but from the entire Great Lakes.) Another instance of alteration of Lake Erie stock is reported by Scott and Crossman (1964), who show that in Hogan's Pond, Newfoundland, whitefish originating from a transplant of Lake Erie fish made 74 years ago had significantly higher gill-raker counts than had their parental stock. Svardson also records various transplants that produced offspring in the new environment with gill rakers different from those of their parental stocks. The parental individuals may have been genetically atypical, but so might they be in a naturally occurring invasion of new waters by a few stray whitefish. McCart and Anderson (1967) also showed in sockeye that gill-raker counts of transplanted progeny differed from those of their parents. We must agree with Svardson (1965) that "the gillrakers are so far the most suitable markers of whitefish populations, giving generalized information about the genetic status of the population concerned." At the same time we must expect that gill-raker counts may vary somewhat between different populations having a common parentage, as a result of some environmental modification and of some genetic selection. Number and length of gill rakers are intimately associated with feeding habits, and may be expected to change through selection along with changes in diet.

Gill-raker counts referred to in the key and the distribution map are "modal" counts, i.e., the most commonly occurring count in the sample. Considerable variation around this mode must be expected. Usually about three-quarters of the counts will fall within one unit either side of the mode, but occasional individuals may have raker counts three or even more above or below the modal count. Provided there is only a single mode, all individuals in the sample may be taken as belonging to the species characterized by the modal gill-raker count.

Other characters so far studied, such as colour, body shape and size, and growth rate, are known from transplants to be extraordinarily plastic in whitefishes, and so are unreliable in sorting out species relationships within this complex. Behavioural traits such as spawning time and place may be important in keeping sympatric species separate, but we are still largely ignorant of such matters. Imaginative search is needed for new taxonomic characters, including biochemical and cytological ones.

Gill-raker counts as well as other characters suggest that the "*Coregonus clupeaformis*" complex includes more than one species, for there are several North American lakes said to contain more than one type of humpback whitefish. The two forms inhabiting Squanga Lake, Yukon Territory, differ in gill-raker count and several other morphological characters; they occupy different depths, take different foods, and probably spawn at different times (Lindsey, 1963b). Although a few individuals appear to be hybrids, the two forms largely retain their separate identities and behave as two distinct species.

Fenderson (1964) found in several Maine lakes that a slow-growing dwarfed form with high gill-raker count lived sympatrically with a faster-growing, larger-maturing form with fewer gill rakers. The two differed in body proportions and in their erythrocyte antigens. In Lake Opeongo, Ontario, Kennedy (1943) found a slow-growing form with fewer gill rakers, which sometimes inhabited slightly deeper water than the "normal" form in the lake. Dragon Lake near Quesnel, British Columbia, probably contained two forms with different gill-raker counts, but these have been eradicated by poison to promote sport fishing for trout. In Great Slave Lake and in Lake Athabasca a dark terete form of whitefish has been reported along with the typical deep-bodied form (Rawson, 1947b), but whether these are genetically distinct is unknown. Kennedy (1953) also refers to the possible occurrence of dwarf whitefish in Great Slave Lake, including a sexually mature female weighing only 2 oz.

Probably we are dealing with several types of whitefish that evolved while isolated around the periphery of the ice sheet during successive Pleistocene glaciations. Whether a pair of forms when reunited will retain their identity and thus behave as two good species, or whether they will interbreed to form a single intermediate form, may depend on how varied are the ecological niches available in a given water body (Svardson, 1957). As a third alternative, partial introgression may occur, so that modal characters of the two forms may approach each other more closely than they do when the forms are geographically separated, and yet the two do not merge completely.

Despite these difficulties, we see some pattern to North American variation in modal gill-raker counts (shown in the distribution map). Most humpback whitefish samples from Bristol Bay drainages, Kuskokwim River, and Alaskan coastal drainages from Bering Strait north, and from Dezadeash Lake, Alsek River system, have low modal counts (20–22, sometimes 23). These conform to counts reported for *Coregonus pidschian* (named by Gmelin in 1788 as *Salmo pidschian* from the Ob River of Siberia).

On the other hand, most samples from the eastern half of our area have high modal counts (26 or more). High counts characterize almost all other North American humpback whitefish samples across the rest of the southern and eastern sections of their range, and also in British Columbia drainages and in Lake Louise on the Susitna River system in Alaska; these all agree with *Coregonus clupeaformis* (named by Mitchill in 1818 as *Salmo clupeaformis* from Sault Ste. Marie on the Great Lakes).

Throughout most of the Yukon River, in Paxson Lake, Copper River system, and sporadically around the coast of northern Alaska, in the Mackenzie River delta and in Anderson River, occurs a form with intermediate modal gill-raker counts (about 24 or 25). If this is a distinct species it should probably be called *C. nelsoni* (so named by Bean in 1884 from Nulato on the Yukon River; see Lindsey, 1963a). The two sympatric species in Squanga Lake on the upper Yukon River may be *C. nelsoni* (there with modal count of 23) and *C. clupeaformis* (with modal count of 28).

Alternatively, *C. nelsoni* may simply represent hybrid populations arising from fusion of *C. pidschian* and *C. clupeaformis.* If so, in Squanga Lake these two may have remained distinct, the former somewhat introgressed so as to have slightly higher raker counts there than it does where it occurs alone around the Bering Sea.

Other names applied to humpback whitefish in our area, including *C. richardsoni* and *C. labradoricus,* are probably synonyms for one of the species already mentioned.

Attempts to delineate subspecies within our area are premature. Also, attempts to extrapolate to localities outside our area (e.g., to attempt to equate the Maine dwarf form with *nelsoni* or *pidschian*) seem to us unjustifiable in our present state of ignorance. Eventually the nomenclature of Old World and New World species must be aligned. *Coregonus clupeaformis* has been tentatively equated to three different Eurasian species by three different recent authors (*C. lavaretus* suggested by Walters (1955) and Reshetnikov (1963); *C. nasus* suggested by Svardson (1957); *C. pidschian* suggested by Gasowska (1960)). We prefer to follow Starks (1926) who wrote, of fish classification, "A question would better remain in the form of a question than in the form of an incorrect answer."

Important contributions may be made to unravelling the taxonomy of humpback whitefishes if persons observing the apparent occurrence of two distinct types of fish (particularly types that spawn separately) will draw such situations to the attention of biologists.

Postglacial Dispersal

The humpback whitefish with low gill-raker count, referred to here as *Coregonus pidschian*, evidently survived Pleistocene glaciation in western Alaska as well as in Siberia, and is now distributed from Bristol Bay around to arctic Alaska. A form with high gill-raker count, referred to here as *C. clupeaformis*, probably survived in the Great Lakes region and has since spread northward across Canada to the Arctic Ocean and westward into some Pacific drainages as far south as the upper Fraser River. This high-count form penetrated the headwaters of the Yukon River. Possibly it has spread downstream to the mouth of the Yukon River, hybridizing in most places with *C. pidschian* to produce intermediate raker counts. *Coregonus pidschian* may also have moved eastward along the arctic coast to the lower Mackenzie, where again some populations with intermediate counts suggest hybridization. Alternatively, the intermediate populations may represent a third species, *C. nelsoni*, which survived in the lower Yukon River and has since spread to Copper River and to a few coastal areas as far east as the Mackenzie and Anderson. The picture may be yet more complex, for refuges in Bristol Bay, arctic Alaska, and farther east may each have contained somewhat different forms of humpback that have variously spread and fused after deglaciation. Another species of whitefish with 23–27 gill rakers occurs in Nova Scotia (Leim and Scott, 1966), but its terminal mouth suggests that it is not the progenitor of any of the humpback whitefish in our area.

Biology

Humpback whitefish occur typically in lakes, although some are taken in the larger rivers, and some migrate out into brackish water. Maximum catches of humpbacks during experimental netting on Great Slave Lake were at depths of 10 m (30 ft), but some were taken as deep as 100 m (Rawson, 1951). Squanga Lake whitefish occur from the surface down at least to depths of 24 m (80 ft); in this lake individuals with low gill-raker count were most abundant close to the bottom at all depths sampled, whereas fish with high raker count were most abundant close to the surface over deep water (Lindsey, 1963b). Both types showed a marked onshore movement at night. In Great Slave Lake young whitefish were frequently taken in seine hauls along shore (Rawson, 1951).

In many localities, humpback whitefish are bottom feeders, taking molluscs and larval insects. In Great Slave and Athabasca lakes the shrimp *Pontoporeia* makes up over half the diet, with the remainder minute snails and clams and some chironomid larvae. In Squanga Lake the form with low gill-raker count ate mostly bottom organisms (clams, snails, chironomid larvae, and the plant *Chara*), whereas the form with high raker count ate mostly pelagic and surface food (small crustacean plankton and some terrestrial insects).

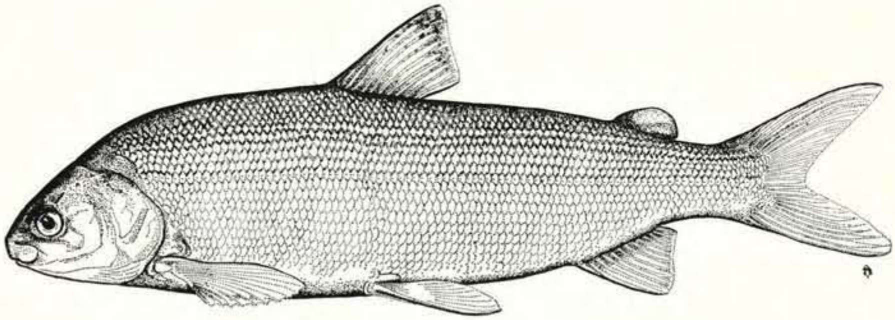
Humpback whitefish reach a weight of 0.9–1.4 kg (2–3 lb) in their 10th year in many northern lakes (including Athabasca, Great Slave, Nueltin, and Great Bear); in MacEwen Lake west of Hay River they reach 3.2 kg (7 lb) at this age. One fish from Great Slave Lake lived to 28 years of age. In Great Slave and Great Bear lakes about half the fish of both sexes mature in their 8th year; in more southerly lakes maturity comes at an earlier age. There is reason to suspect that in some northern lakes individual female whitefish may spawn only every 2nd year.

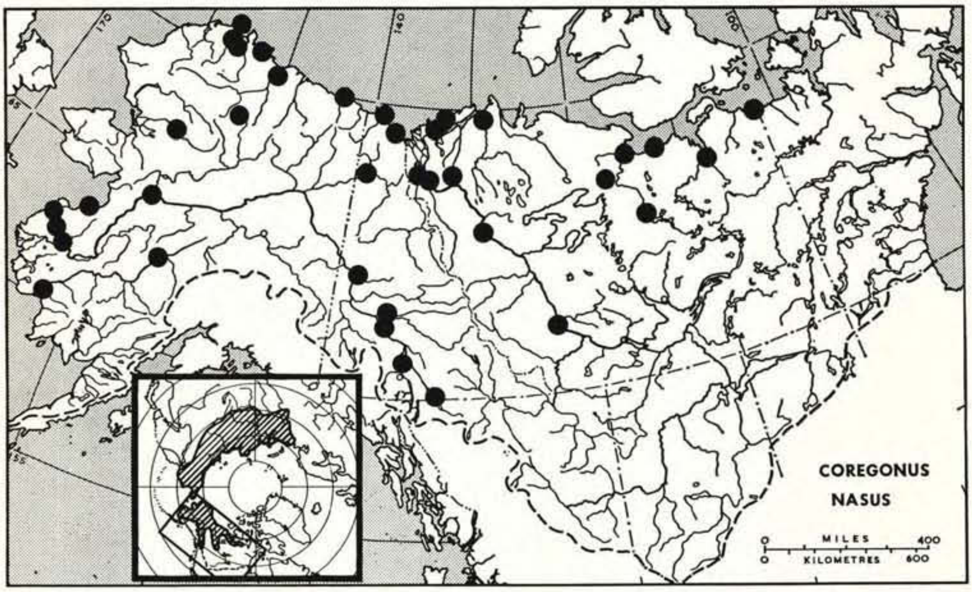
Spawning may occur from late summer to at least as late as November or December. In Great Slave Lake whitefish spawn from mid-September to mid-October. Spawning usually occurs over rocky reefs in lakes or in the shallows of rivers. In Squanga Lake the form with high gill-raker counts spawns both in the inlet and outlet streams in November and December; the form with low raker counts probably spawns later. In coastal areas an upstream migration may occur in autumn prior to spawning. Each female sheds tens of thousands of yellowish eggs, which hatch during the late winter or following spring.

Of whitefish as food, Sir John Richardson (1836a, b) wrote: "Though it is a rich, fat fish, instead of producing satiety it becomes daily more agreeable to the palate; and I know, from experience, that though deprived of bread and vegetables, one may live wholly upon this fish for months, or even years, without tiring. The stomach, when cleaned and boiled with the rest of the fish, is a favourite morsel with the voyageurs." Whitefish apparently provides a nearly balanced diet; the pioneers who lived on whitefish were not afflicted with deficiency diseases such as scurvy.

Gillnet fisheries for whitefish have existed for many years throughout the north, for local consumption by man and sled dog. A few whitefish are taken in fishwheels along the Yukon River. Important commercial gillnet fisheries have now developed on several lakes in the Canadian north, which provide fresh whitefish for transport by air or truck to southern markets. Between 1945 and 1954 the Great Slave Lake fishery produced 35 million lb of whitefish. The excellence of the product commands a high price on the export market.

In some lakes the flesh of whitefish contains cysts of the tapeworm *Triaenophorus crassus*, which, although harmless to man, are unsightly and destroy the market value. The adult tapeworm lives in the intestine of the northern pike. Here it matures and releases its eggs in the spring. The eggs hatch and infect the minute crustacean *Cyclops*. Infected *Cyclops*, when eaten by whitefish or ciscoes (or by lake trout), carry the parasites to these fish, where they develop into the cysts. The life cycle is completed when a pike swallows a fish containing cysts. Incidence of infection in whitefish varies greatly between different lakes, depending on such factors as the number of pike and the amount of contact between whitefish and infected *Cyclops*. No satisfactory control system has yet been perfected, but intensive fishing for pike gives promise of substantially lowering the incidence of cysts in whitefish in the same lake. Meanwhile a system of Government inspection has been devised to control the sale of infected fish, based on "candling" the flesh against a bright light to assess the number of cysts. Cysts may be cut from the flesh or removed by a suction device. It should be stressed, however, that they constitute absolutely no hazard to man.




COREGONUS
NASUS
MILES
400
KILOMETRES
600

BROAD WHITEFISH

Coregonus nasus (Pallas)

Nasus refers to the shape of the nose. The French common name for this species is *corégone tschir*.

Distinguishing Characters

Tip of snout blunt, projecting slightly beyond tip of lower jaw; body flat-sided, not round in cross section; brow rounded, not concave in profile; gill rakers shorter than one-fifth the space between eyes.

Description

Body compressed, the sides flattened. Head short, usually more than four times into length. Dorsal profile of head not concave (Fig. 16A), or slightly so in some large specimens. Adipose eyelid without a ventral notch. Profile of upper lip vertical, or sloping slightly down and back. Snout blunt and "sheep-nosed" in appearance; maxilla usually ending at or before a vertical line through the anterior edge of eye, but sometimes reaching behind it; maxilla length 19–23% of head length; maxilla 1.9–2.6 times maxilla width; maxilla length less than three-quarters of interorbital width in fish over 25 cm standard length (fork length about 11 inches); in smaller fish, maxilla length less than four-fifths of interorbital. Basihyoid bone with patch of weak bristlelike teeth. Head deeper, more foreshortened and wider than in humpback whitefish; body and caudal peduncle deeper; adipose fin sometimes very large. Double flap between the nostril openings. Branchiostegal rays 8 or 9 on either side. Total gill-raker counts examined by us 21–25 (8–10 + 12–15), but reported by others to be as low as 18; length of longest gill raker 0.85–1.35% of standard length, or 13–19% of interorbital width (Fig. 17A). Dorsal fin with 10–13 major rays; anal with 11–14 major rays. Scales large, cycloid, 84–102 pored scales in lateral line, 9–11 in suprapelvic row, 25–29 scale rows around caudal peduncle. Vertebrae not counted in our area, reported in the Lena River to be 62–65, usually 64 or 65. Pyloric caeca about 148.

Size: Total weight in Canada reported "over 4 lb or 2 kg," in USSR occasionally up to 16 kg (35 lb). A fish 59.4 cm (23.4 inches) total length was taken from Anderson River. A 3.7-kg (8.1-lb) specimen from the Lena River was 67.5 cm (26.6 inches) long.

Sexual dimorphism: Males at spawning time develop rows of hard white conical tubercles on the scales; these are probably less numerous in females. The first ray of the pectoral fin of females is said to become white, whereas other rays of this fin remain dark.

Colour: Brown or blackish on back, belly yellowish. In some waters the whole fish may be silvery, but often it is quite dark, with dark patterns along the scale rows. Fins often dark, but without distinct patterns. Young pale, without parr marks.

Distribution

In Eurasia, in Arctic Ocean drainages from Bering Strait west to the Pechora River and possibly into northern Europe, and south on Bering Sea to the Bay of Korf, and in the Penzhina River on the Sea of Oknotsk. Ascending the great Arctic Ocean drainages of the USSR only to a short distance south of 60°N lat.

In North America, in Bering Sea drainages south to the Kuskokwim River, in the Yukon River to its headwaters in British Columbia, and in northern Bering Sea and in Arctic Ocean drainages as far east as Perry River. Ascending the Mackenzie River to Camsell Bend at about 62°N. Not recorded from North American islands of the Bering Sea or Arctic Ocean except Herschel Island. Sometimes taken in brackish water.

Taxonomic Notes

Pallas named *Salmo (Coregonus) nasus* from the Bay of Ob in 1776. In the New World it has often been called *Coregonus kennicotti* or *Coregonus nasus kennicotti.* Dymond (1943) and others doubted the specific distinctness between the broad whitefish and the humpback whitefish *C. clupeaformis.* However, examination of specimens from 15 North American localities where the two kinds occur sympatrically has shown that *C. nasus* is a distinct species (Lindsey, 1962). Svardson (1957) has reviewed the systematics of Eurasian species, and suggested that *C. clupeaformis,* amongst others, is a synonym for *C. nasus.* His synonymies are based largely on gill-raker count, and in this instance are doubtful, as there are several localities in our area where *C. nasus* and humpback whitefish are similar in gill-raker numbers but very different in gill-raker length, interorbital width, and many other characters.

The large whitefish described by Bajkov (1927) from Beauvert Lake in Jasper Park, Alberta, as *C. nasus,* and named by Berg (1932) as a new subspecies, *C. nasus canadensis,* was probably an aberrant *C. clupeaformis* (Lindsey, 1962).

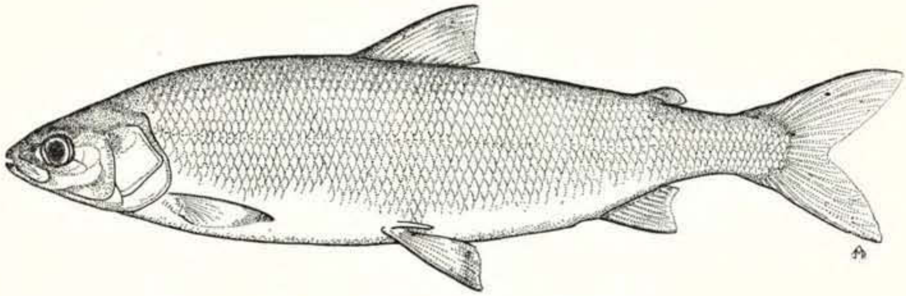
Postglacial Dispersal

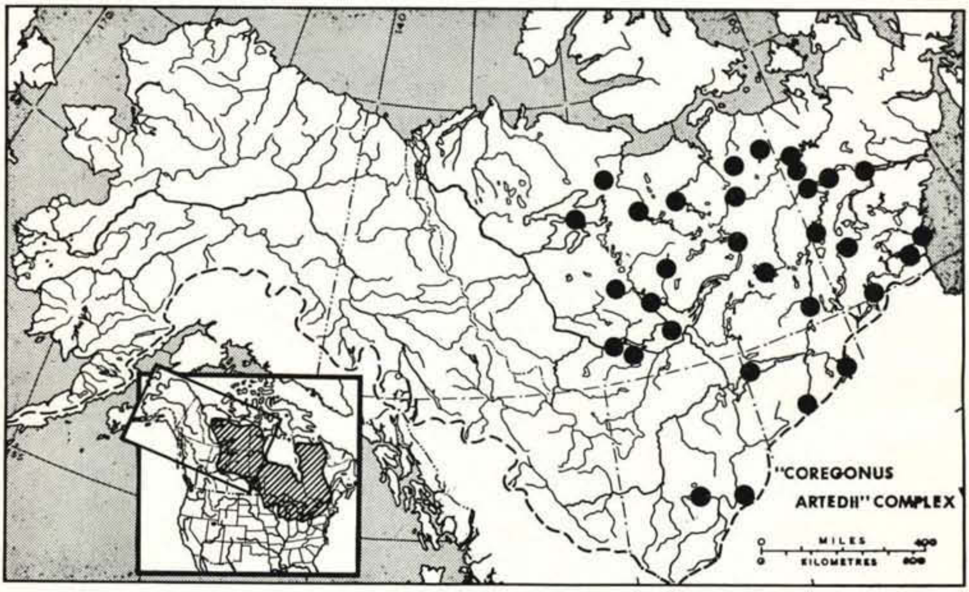
The broad whitefish evidently survived glaciation in the Bering region and perhaps also farther west in Eurasia. It has since spread east along the arctic coast as far as Perry River. It is apparently a cold-adapted species, whose southern limit in both Eurasia and North America is roughly 60°N.

Biology

The broad whitefish occurs mostly in rivers, sometimes in lakes; in some areas it is evidently anadromous, venturing at least into brackish water. Little is known of its habits. Berg (1932) writes that in some waters in Russia its young apparently perform several migrations from the lakes to the rivers and back. As is suggested by its short gill rakers and blunt snout, it is apparently a bottom feeder, eating molluscs and aquatic insect larvae. Age has apparently not been recorded as yet in North American broad whitefish; in the Kolyma River delta fish reached 35 cm total length (weight 0.38 kg) at age 4, 45 cm (0.96 kg) at age 6, and 62 cm (2.56 kg) at age 9 (Berg, 1948–49). An upstream spawning run of broad whitefish is said by Wynne-Edwards (1952) to occur in July and August in the lower Mackenzie River, coming somewhat earlier than that of the humpback whitefish. In the Yukon River it has been reported to enter small tributary streams to spawn in September. A specimen taken on October 4 from Yukon River near Dawson City had tubercles and well-developed eggs. The eggs are paler than those of the humpback whitefish.

In the summer fisheries around the Mackenzie River delta the broad whitefish is said to be about twice as plentiful as the humpback, and grows to a larger size. However, in the Yukon as well as the Mackenzie it is at present taken only for local consumption. Wynne-Edwards wrote of this fish in 1947: "A word of explanation may be given here on the subject of the "tezra" or "tizareh", a fish renowned in the Yukon for its palatability and delicate flavour. In the days of the winter mail-stages, which ended about twenty years ago, whitefish caught by Indians in Minto lakes were carried frozen to Dawson and Whitehorse, and known by this Indian name. Actually the tezra is the Mackenzie (broad) whitefish; it enjoys an equal reputation along the Mackenzie, and is quite possibly the finest freshwater table-fish in Canada."




"COREGONUS
ARTEDII" COMPLEX
MILES
KILOMETRES

LAKE CISCO

"Coregonus artedii" complex including *Coregonus artedii* LeSueur

Artedii is named for Petrus Artedi, the "Father of Ichthyology." The French common name for this species is *cisco de lac.*

Distinguishing Characters

Lower jaw usually projects beyond upper jaw when mouth closed, and prepelvic distance when stepped backwards with dividers falls on caudal fin base or caudal fin, behind the caudal flexure.

Description

There is considerable variation in the ciscoes that will be identified as "*C. artedii*" complex in our key. Most of this variation is geographic and may be mainly phenotypic. However, there are a number of lakes in which at least two forms exist sympatrically, and undoubtedly more than one species of cisco is included under the name "*C. artedii*" complex. The following description includes all forms.

Body elongate, somewhat compressed; head moderate, about one-quarter standard length; eye moderate, about 4 into head; snout usually equal to horizontal eye diameter. Adipose eyelid with a ventral notch. Profile of upper lip sloping up and back in line with forehead; tip of lower jaw usually projects beyond tip of upper when mouth closed. Mouth moderate, maxilla extending back to about middle of pupil; maxillaries, vomer, and palatines toothless; a narrow patch of small teeth on the tongue and weak teeth in the lower jaw of adults in some populations. Double flap between the nostril openings. Branchiostegals 7–10 + 8–10; gill rakers long and slender, total counts 41–51 (14–18 + 27–33). Pelvic fins inserted far back; distance from snout to front of pelvic base equals distance from front of pelvic base to a point on the caudal rays posterior to the caudal flexure (Fig. 12A). Dorsal fin with 12–14 major rays; 11–14 major anal rays; 14–16 pectoral rays; and 8–12 pelvic rays. Scales large, cycloid, 67–89 pored scales in the lateral line. Vertebrae 56–63; 80–162 pyloric caeca.

Size: Up to 55 cm (21½ inches) and 3.6 kg (8 lb) in Lake Erie (Scott, 1958), but usually much smaller. In our area the largest specimens are about 46 cm (18 inches) long, but in some lakes (e.g., Gordon Lake near Yellowknife) mature adults are less than 15 cm (6 inches) long.

Sexual dimorphism: Rows of tubercles are present on the sides of spawning males, but are absent, or only weakly developed, in females.

Colour: Adults are dark blue to green or brown above and bright silver below. The dorsal and caudal fins are mostly light but often dusky towards tips. The paired fins and anal fin are usually immaculate, although the pelvic fins in some populations are often tipped with black. The young are coloured like the adults and have no parr marks.

Distribution

Known only from North America. From the upper Mississippi system and the Great Lakes northward into Labrador and to the northwest at least as far as the Mackenzie system. Enters coastal salt water in Hudson Bay. In our area, common in most lakes on the Barren Grounds, and in the Mackenzie system from Great Bear Lake south, but not recorded from the Liard or Peace river drainages.

Taxonomic Notes

The lake cisco was first named as *Coregonus Artedi* by LeSueur in 1818, based on specimens from Lake Erie and the Niagara River. In the past the generic names *Leucichthys* or *Argyrosomus* have been used for ciscoes; reasons for using the name *Coregonus* are given in introductory notes for the family. Five species of ciscoes that have been named from our area are possibly synonymous with *C. artedii*: *C. lucidus* (Richardson) from Great Bear Lake; *C. athabascae* (Harper and Nichols) from Athabasca Lake; *C. micrognathus* (Harper and Nichols) from Great Slave Lake; *C. entomophagus* (Harper and Nichols) from the Tazin River (this species may be valid); and *C. nueltinensis* (Fowler) from Nueltin Lake. In addition, *C. tullibee* (Richardson) named from central Saskatchewan is usually considered a synonym of *C. artedii*, although Preble's (1908) *Argyrosomus tullibee* of the lower Mackenzie is probably *C. autumnalis*.

The recognition of a *"Coregonus artedii"* complex is intended as middle ground between two extremes: either the arbitrary designation of all northern ciscoes of the *C. artedii* type (ciscoes with about 40–50 gill rakers in which the prepelvic distance, if stepped off with dividers, falls either on the caudal fin or the caudal fin base) as a single widespread polymorphic species, or the recognition of a host of species and subspecies based on geography and little else.

The first alternative (a single polymorphic species) would be an oversimplification. There are several lakes in the Northwest Territories that are known to contain sympatric populations of at least two forms of *artedii*-like ciscoes. Although there are undoubtedly many such situations, none has been studied carefully. One lake that may contain a sympatric pair of *artedii*-like ciscoes is Beverly Lake in the district of Keewatin. The ciscoes in this lake fall into two size groups at sexual maturity: a small form that matures at about 150 mm, and a much larger form that matures at about 300 mm. The two kinds appear also to differ in mean gill-raker number (the smaller fish have more gill rakers) and differ quite markedly in number of pyloric caeca (the small fish have 90–120 pyloric caeca, the large fish 147–160). Although the sample available from this lake is small, about 30 fish in total, it is suggestive of a sympatric pair of ciscoes. A similar situation exists in Kathawachaga Lake in the district of Mackenzie, and both Rawson (1947) and Kennedy (1949) have suggested sympatric forms of ciscoes in Great Slave Lake, Great Bear Lake, and Lake Athabasca. Possibly the second species is in some instances a member of the *"C. sardinella"* complex, which according to our current interpretation is everywhere allopatric to the *"C. artedii"* complex. Samples from Churchill on Hudson Bay are also very variable and may include more than one species.

The five species of *artedii*-like ciscoes originally named from our area have been listed above. Also *C. tullibee*, named from central Saskatchewan, has been recorded from our area. In addition, three Great Lakes species have been recorded from our area (*C. artedii, C. nigripinnis,* and *C. zenithicus*). Of these nine species, six fall into the *"C. artedii"* complex, as defined above; *C. entomophagus, C. nigripinnis*, and *C. zenithicus* probably do not.

Coregonus zenithicus has been recorded from Lake Athabasca (Dymond and Pritchard, 1930), and Dymond (1943) suggests that *C. entomophagus, C. athabascae,* and *C. macrognathus* are all conspecific with *C. zenithicus*. However, Dymond apparently miscounted gill rakers on the holotypes of these species (they have been re-examined by Dr D. E. McAllister, National Museums of Canada) and Dymond's counts are consistently low. *Coregonus macrognathus* has 42 gill rakers, *C. entomophagus* 37, and *C. athabascae* 40+ (the gill arches are damaged on the holotype). Except for *C. entomophagus* with 37 gill rakers, the other species fit into the *"C. artedii"* complex and probably do not represent *C. zenithicus*. The gill-raker count of *C. entomophagus* places it just below the normal range of the *"C. artedii"* complex suggesting that it may represent a distinct species. Whether it is one of the low gill-raker species of the Great Lakes region, or a separate species, can be clarified only by further study, particularly in the intervening areas. The same is true for Rawson's (1947 and 1951) records of *C. nigripinnis* from Lake Athabasca and Great Slave Lake. It is entirely possible that *C. nigripinnis* does occur in the upper Mackenzie system. This species has virtually the same gill-raker count (41–52) as *C. artedii*. In the Great Lakes where it occurs sympatrically with *C. artedii* it spawns later in the year (December to January) and is much deeper-bodied than *C. artedii*. However, in Great Slave Lake the form Rawson tentatively called *C. nigripinnis* is described as being a slender species.

Without a great deal more morphological and ecological data on the ciscoes of the upper Mackenzie system and the intervening area between there and the Great Lakes, it is futile to attempt to equate species in the two areas. In assigning all of the *C. artedii*-like ciscoes in our area to the "*C. artedii*" complex, we recognize that several species are probably involved, and hope that this unsatisfactory situation will soon be corrected by further research.

Postglacial Dispersal

The geographic distribution of the "*C. artedii*" complex as defined here includes only one glacial refuge, the upper Mississippi. All of the populations in our area were probably derived by northward postglacial dispersal from this source. These ciscoes are well-suited for life in cold, deep lakes, and probably attained their present wide geographic range through the complex series of proglacial lakes that were formed in central Canada by the retreating ice sheets.

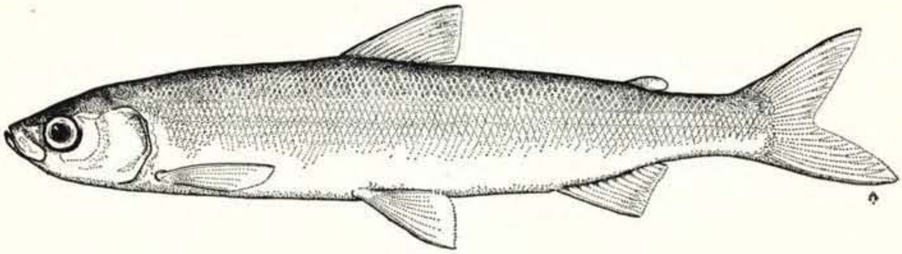
Biology

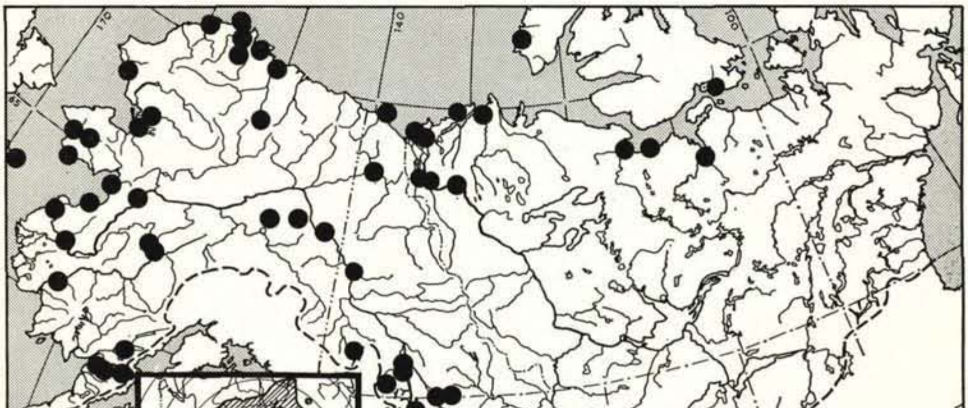
The ciscoes of the "*C. artedii*" complex are found mainly in lakes. They occur in large shoals, and are often common both in shallow and deep water. Adults feed mainly on plankton and large crustaceans (*Mysis* and *Pontoporeia*), but also on chironomid larvae and occasionally on young fish. Spawning occurs in late autumn over sandy or gravel shallows. The eggs are simply scattered over the bottom. In Great Bear Lake ciscoes mature in their 5th or 6th year, but may not spawn every year after reaching maturity (Kennedy, 1949). The oldest known specimen from our area reached 14 years of age.

Much has been written on the feeding, growth, and migrations of *C. artedii* in more southerly areas (Hile, 1936; Fry, 1937; Langford, 1938). We do not know how much of such information on life history is applicable in our area, for we do not know whether the same species are involved. Ultimately, studies on ecological rather than morphological differences are likely to clarify the interrelationships within this complex, particularly in northern lakes containing sympatric forms.

Ciscoes are tasty and nourishing. In the lower Mackenzie and Great Bear lake regions it is claimed that man and dogs can subsist all winter exclusively on this fish.

At the western end of Great Bear Lake the second Franklin expedition took great numbers of ciscoes in 1825–26; since then the Hudson's Bay and other trading companies, as well as the missions, have regularly established a fishery at the same place, and a continuous "herring" fishery still persists at Fort Franklin. In Lesser Slave Lake, Alberta, several million pounds of ciscoes are taken annually for mink food.




"COREGONUS SARDINELLA" COMPLEX
MILES 400
KILOMETRES 600
140
100
170

LEAST CISCO

"*Coregonus sardinella*" complex
including *Coregonus sardinella* Valenciennes

Sardinella means *small sardine*. The French common name for this species is *cisco sardinelle*.

Distinguishing Characters

Lower jaw projects beyond upper jaw when mouth closed, and prepelvic distance when stepped backwards with dividers falls on caudal peduncle ahead of caudal flexure.

Description

In our area there are at least two well-marked forms within the "*C. sardinella*" complex. One form is large and is often caught in or near the sea, whereas the other form is small and usually found in lakes. The following description includes both forms. The distributions and morphological differences between these forms are discussed under "Taxonomic Notes."

Body troutlike, somewhat compressed; head moderate, usually more than 4 times into standard length; eye large, usually less than 4 into head. Adipose eyelid with a ventral notch. Profile of upper lip slopes up and back; tip of lower jaw projects beyond tip of upper when mouth closed; snout usually less than eye diameter. Mouth moderate, maxilla extending back to about middle of pupil; maxillaries, vomer, and palatines toothless; a well-developed patch of small teeth on the tongue; no basibranchial teeth. Double flap between the nostril openings. Branchiostegals 8–9 + 8–9; gill rakers long and slender, total counts 42–53 (14–18 + 28–35). Pelvic fins inserted forward; distance from snout to front of pelvic base equals distance from front of pelvic base to a point on the caudal peduncle ahead of the caudal flexure (Fig. 12B). Dorsal fin falcate, with 12–14 major rays; 11–13 major anal rays; 14–17 pectoral rays; and 8–12 pelvic rays. Scales large, cycloid, 78–98 pored scales in the lateral line. Vertebrae 58–64; 74–111 pyloric caeca.

Size: The size of least ciscoes varies widely with the area. The migratory form reaches 42 cm (16½ inches) in length, whereas the nonmigratory form seldom is larger than 23 cm (9 inches).

Sexual dimorphism: There are no known external differences between the sexes, but spawning males probably develop tubercles along the sides.

Colour: Adults are brown to olive green above and silvery below. The large, apparently anadromous, form of least cisco has dark spots on the dorsal and adipose fins as well as on the back and head. The pelvic and anal fins in this form are usually tipped with black pigment and the leading edge of the pectoral fin is dark and sometimes spotted. In the smaller nonmigratory form there are no spots on the fins or back. All of the fins are immaculate except for the pelvic fins, which are often tipped with dark pigment.

Distribution

Western North America and Siberia (from the Anadyr River westward along the arctic coast to the Pechora River and the extreme headwaters of the Volga River). In our area from Bristol Bay throughout Alaska and eastward along the arctic coast at least to Bathurst Inlet and Cambridge Bay. In the Northwest Territories this species apparently does not penetrate very far inland. It has been recorded from the Mackenzie River only as far upstream as Fort Simpson, and is apparently absent from most of the lakes on the Barren Grounds. (The ciscoes in the Barren Ground lakes apparently belong to the *"C. artedii"* complex.) Present on St. Lawrence Island in Bering Sea, and Victoria and Banks Island in the Arctic Ocean.

Taxonomic Notes

The least cisco was first described as *Coregonus sardinella* by Valenciennes in 1848 on the basis of specimens from the Irtysh and Kolyma rivers in Siberia. In the past, the generic name *Leucichthys* has been used for the ciscoes. Reasons for using the name *Coregonus* are given in the introductory notes for the family. *Coregonus pusillus* named by Bean in 1889 from the Kobuk River, Alaska, is a synonym.

As mentioned earlier, there are two well-marked forms of *"C. sardinella"* in our area. One form is apparently anadromous (or at least migratory) and reaches a length of about 360 mm; the other is nonmigratory and seldom exceeds 220 mm. The dorsal fin, and often the back, of the anadromous form is usually heavily spotted whereas the dorsal fin and back of the nonmigratory form are never spotted. The large, spotted form has 48–53 gill rakers with a mean usually near 50; the small nonmigratory form has from 41 to 47 gill rakers with the mean usually near 45. The only known exception are the populations of unspotted, nonmigratory ciscoes in Lake Iliamna and the Naknek area of the Bristol Bay region in Alaska. These populations are unusual in other ways and will be dealt with later.

The distributions of the two forms of *"C. sardinella"* ciscoes are essentially allopatric. The large, spotted form is found mainly in coastal regions from Bristol Bay north and east to about Bathurst Inlet. This form ascends the Yukon at least as far upstream as Circle. The smaller form is mainly lacustrine and is abundant in the large lakes of the upper Yukon, but it is also commonly found in large rivers in the upper Yukon system. Probably both forms occur sympatrically in parts of the Yukon system at certain times of the year.

The ciscoes in Naknek Lake (a Bristol Bay drainage) are noteworthy on two counts. Firstly, their presence in Naknek Lake is odd in that there are no ciscoes in the large lakes of the Woods River system on the north side of Bristol Bay, although the same form is present in Iliamna Lake. Secondly, their morphology is unusual. They appear to be a dwarf form (the largest we have seen is less than 150 mm in standard length) and they have an extremely high gill-raker count (49–53 in a sample of 25). Since parts of the Bristol Bay region were unglaciated, it is possible that the Naknek and Iliamna lake ciscoes represent a form endemic to that region. This suggestion is supported by the presence of an endemic form of *Prosopium* in the same region (see discussion under *P. coulteri*).

Preble (1908) writes that *Argyrosomus lucidus* occurs in Great Bear Lake and in the Mackenzie River as far upstream as Fort Simpson; the species in the former locality is probably in the "*C. artedii*" complex, but the latter (migratory) species is probably in the "*C. sardinella*" complex. As mentioned under "*C. artedii*" complex, some northern Canadian lakes other than those shown on the map for "*C. sardinella*" complex probably contain the latter species where it is sympatric with a member of "*C. artedii*" complex.

The species complexes *Coregonus sardinella* and *C. artedii* are largely allopatric, and their distinction has rested on morphological grounds that are not as clear-cut as might be wished. New evidence based on biochemical data now lend independent support to the belief that these forms are indeed different. Electrophoretic analysis of blood samples of *C. sardinella* in Lake Laberge, Y.T., shows that their cathodal haemoglobin bands are distinctively different from those in samples of *C. artedii* from several central Canadian lakes (J. W. Clayton, personal communication). It has yet to be established with certainty that haemoglobin banding patterns are not subject to environmental modification, but accumulating evidence suggests that such characters will be a useful addition to morphological characters in coregonid taxonomy. In this instance, biochemical evidence so far supports a taxonomic conclusion previously reached on morphological grounds.

Postglacial Dispersal

The present distribution of "*C. sardinella*" suggests that the populations in our area were derived from populations that survived glaciation in the Bering refuge. Most of the North American range of "*C. sardinella*" is confined to the Bering refuge area; the only significant postglacial range expansion has been to the east along the arctic coast of Canada.

Biology

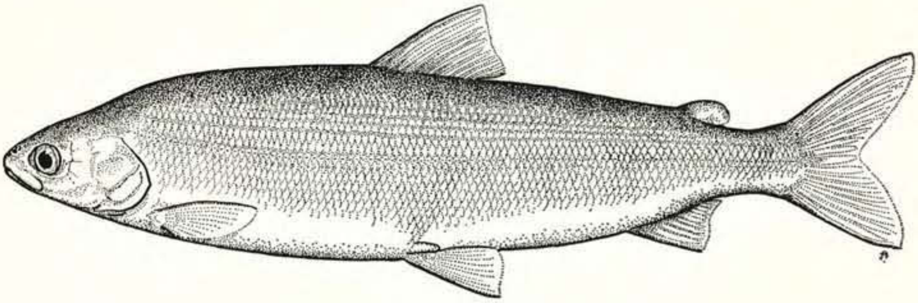
In the western part of our area least ciscoes are very abundant. They occur in almost all large lakes and rivers, in either anadromous or nonmigratory forms. Preble (1908), probably referring to this species, writes "Père Giroux of Arctic Red River informed me that it passes there on its way up the Mackenzie about the second or third week in June, remaining abundant about three weeks; that it is taken nearly all summer about Fort Good Hope; and that it returns to the mouth of the Mackenzie in late autumn. It was just appearing at Fort Good Hope on June 20, 1904. It ascends the river at least to Fort Simpson, and numbers are taken in nets set at right angles to the bank. A special net, having a very small mesh, is necessary for the capture of this species, as it is smaller than any other fish regularly taken in the region. Its excellent flavour and good condition, however, make it one of the most desirable."

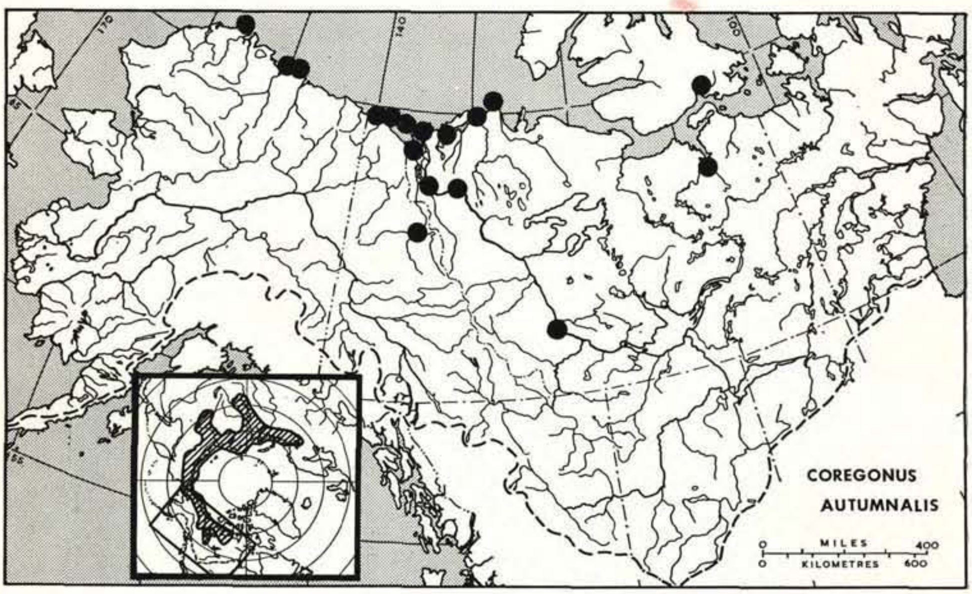
More is known of the biology of the least cisco in the USSR than in North America; most of the following data are derived from works summarized by Berg (1948–49). Anadromous adults are found mainly in the estuaries of rivers and brackish lagoons, and feed primarily on amphipods. According to Berg (1948–49) adults do not feed during their spawning migrations. The nonmigratory adults are common in large lakes and rivers, and feed principally on plankton and insect larvae. Spawning occurs in autumn. Wolschlag (1954) noted a late summer migration near Point Barrow, and natives report that large numbers of ciscoes appear in Birch Creek, near Circle on the middle Yukon, in early autumn. In Siberia both summer and autumn spawning migrations are reported. Spawning occurs over sand and gravel in shallow areas, and the eggs are simply scattered over the bottom. Large females lay from 9000 to 14,000 eggs. These incubate over winter and hatch in late May or early June.

Cohen (1954) has studied age and growth in marine and freshwater populations near Point Barrow, Alaska. In this region marine specimens reach a maximum age of 11 years, whereas freshwater specimens normally do not exceed an age of 9 years. In Siberia, the maximum recorded age is also about 11 years (10+), and sexual maturity is attained at 5 or 6 years. In Teslin Lake, B.C. and Y.T., which contains a nonmigratory form, the oldest recorded fish was 8 years old, 24.9 cm long, and weighed 113 g; the largest was 6 years old, 27.6 cm long, and weighed 312 g.

In the vicinity of Point Barrow, Ikroavik Lake contains a probably nonmigratory form that is fatter, deeper-bodied, and faster growing, in contrast to a migratory form in nearby Elson Lagoon. The latter form, which has higher oxygen consumption and metabolic rates, migrates over distances of at least 100 miles, but returns to fresh water during winter (Wohlschlag, 1953, 1954, etc.). The habit of feeding during summer in the sea and moving up rivers or into lakes for the winter (practiced by Arctic char and smelt as well as by some populations of least cisco) has been suggested by Walters (1955) as an arctic adaptation to escape the low winter temperatures (below 0 C) in sea water.

The migratory form of least cisco supports a major fishery in the lower Kolyma River in Siberia. In North America its small size precludes it from most commercial gillnet fishing, but it is taken in small-meshed nets along the Mackenzie, and local native fisheries exist in a few Arctic rivers such as the Meade. Wynne-Edwards (1952) writes "In the Yukon it is abundant right up to the headwaters, and is best known at Carcross, Y.T., lying in immense schools in summer beneath the railroad bridge across the narrows between Lakes Bennett and Tagish, where children take it on a hook."




170
140
100
COREGONUS
AUTUMNALIS
0 MILES 400
0 KILOMETRES 600

ARCTIC CISCO

Coregonus autumnalis (Pallas)

Autumnalis means *of the autumn*. The French common name for this species is *cisco arctique*.

Distinguishing Characters

The terminal mouth and the intermediate number of gill rakers on the lower limb of the first arch (26–31) characterize this species.

Description

Body troutlike, only slightly compressed; head moderate, usually more than 4 into standard length; eye moderate, less than one head length; snout a little larger than horizontal eye diameter. Adipose eyelid with a ventral notch. Profile of upper lip slopes up and back; tips of upper and lower jaws about equal when mouth closed. Mouth moderate, maxilla extending back to about the anterior margin of pupil. Jaws toothless in adults (young up to about 3 cm have feeble teeth in jaws); vomer and palatines toothless, but a few teeth on the tongue; no basibranchial teeth. Double flap between the nostril openings. Branchiostegals 8–9 + 8–9; gill rakers long, slender, total counts 41–48 (15–17 + 26–31). Dorsal fin with 10–12 major rays; 12–14 major anal rays; 14–17 pectoral rays; and 11 or 12 pelvic rays. Scales large, cycloid, 82–110 pored scales in the lateral line. Vertebrae 64–67; 113–183 pyloric caeca.

Size: Length up to 64 cm (25.2 inches) and weight up to 2.5 kg ($5\frac{1}{2}$ lb) (Berg, 1948–49), but usually less than 51 cm (20 inches) in length.

Sexual dimorphism: No obvious external differences between sexes except at spawning time. Rows of flat tubercles on the sides present in spawning males but absent, or only weakly developed, in females.

Colour: Anadromous adults are brown to light green above and bright silver below. The dorsal and caudal fins are dusky, whereas the paired fins and anal fin are usually immaculate. The young are coloured like the adults and have no parr marks.

Distribution

Northern Europe and Siberia (Velta River east to the Kolyma River, but apparently absent from the Ob River), and western arctic North America. In North America from Point Barrow on the arctic coast of Alaska to Bathurst Inlet, N.W.T., and at Cambridge Bay on Victoria Island; apparently absent from Bering Sea drainages.

Taxonomic Notes

The Arctic cisco was first described as *Salmo autumnalis* by Pallas in 1776 on the basis of specimens from the Kara River, Siberia. In North America the generic names *Argyrosomus* and *Leucichthys* were at one time used for ciscoes. Reasons for using the name *Coregonus* are given in the introductory notes for the family. Until recently the Arctic cisco and *C. laurettae* have been confused by many authors (see "Taxonomic Notes" under *C. laurettae*); *C. autumnalis* in the lower Mackenzie has been called *C. laurettae* by Wynne-Edwards (1952), and *Argyrosomus tullibee* by Preble (1908). The populations of *C. autumnalis* along the western arctic coast of North America appear to be morphologically undifferentiated from those along the arctic coast of Siberia.

Postglacial Dispersal

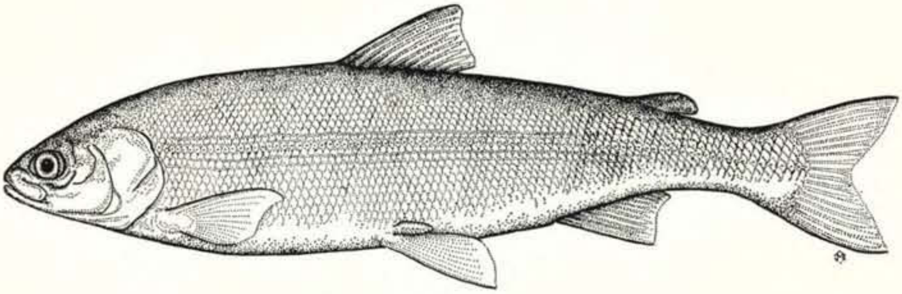
The Arctic cisco has a geographic range that is unique among the fishes in our area. It is the only species whose North American range is confined to the western arctic coast (it is absent from the Bering Sea; records of *C. autumnalis* from that area are based on *C. laurettae*). This distribution suggests that *C. autumnalis* survived the Wisconsin period along the unglaciated arctic coast of Alaska, and has scarcely expanded its North American range postglacially.

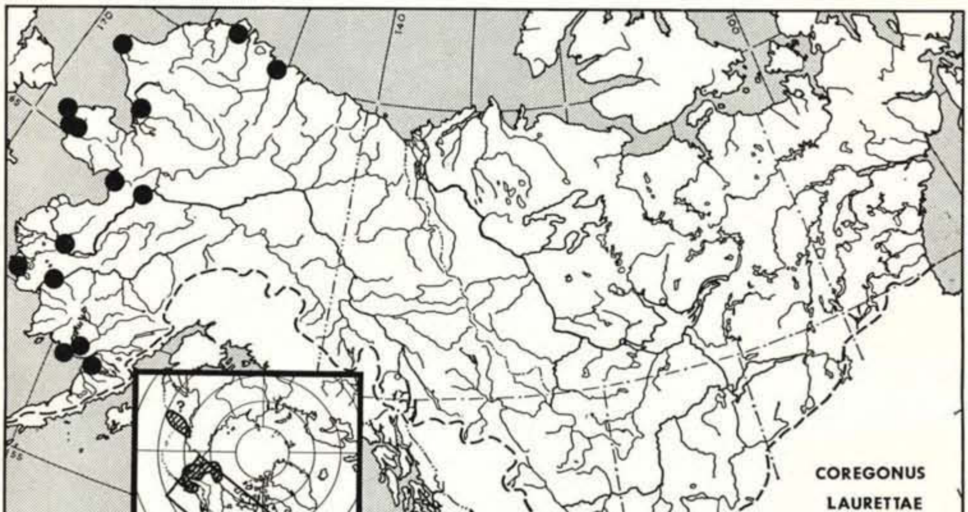
Biology

Arctic ciscoes commonly occur in the lower reaches of large muddy rivers, and are particularly abundant in brackish water areas. Adults feed mainly on crustaceans and small fishes; the feeding habits of the young are unknown. The Arctic cisco is anadromous, and ascends the Mackenzie (up to Camsell Bend), Arctic Red, and Peel rivers in early spring according to Wynne-Edwards (1952). Spawning occurs in late summer and early autumn; we took ripe adults at the junction of the Peel and Caribou rivers on August 1, 1960. Preble (1908) writes "Père Giroux informed me that these fish are extremely abundant at Arctic Red River in September, when they come in from the sea and spawn in very deep basins in the Mackenzie, where as many as a hundred may be taken in a net sunk to the bottom. They remain during October."

Spawning probably takes place over gravel in fast water. No nest is built (Berg, 1948–49), and the eggs are apparently simply scattered over the gravel. Large females carry about 90,000 eggs. After spawning, a distinct downstream migration occurs (on the Mackenzie River between freeze-up and Christmas (Wynne-Edwards, 1952)). Nothing is known about the age and growth of the Arctic cisco in North America. However, in Siberia they mature at about 5 years (although this varies greatly between river systems) and live about 8 or 9 years. Berg (1948–49) indicates that rare individuals reach 17 years of age.

The Arctic cisco is an important food fish on the lower Mackenzie River, and Dymond (1943) writes that it is "well liked as human food and is equal to whitefish as dog food since it is fat most of the year." The Arctic cisco is the main object of a summer fishery at the Ramparts on the Mackenzie and is also caught and dried in large numbers at Arctic Red River and Aklavik (Wynne-Edwards, 1952).




COREGONUS
LAURETTAE
MILES
400
KILOMETRES
600

BERING CISCO

Coregonus laurettae Bean

Laurettae is named for Mrs Lauretta H. Bean. The French common name for this species is *cisco du Bering*.

Distinguishing Characters

The terminal mouth and the low number of gill rakers on the lower limb of the first arch (21–25) characterize this species.

Description

Body troutlike, somewhat round in cross-section; head moderate, usually more than 4 times into standard length; eye moderate, usually more than 4 into head; snout about equal to horizontal eye diameter. Adipose eyelid with a ventral notch. Profile of upper lip slopes up and back; tips of upper and lower jaws about equal when mouth closed. Mouth moderate, maxillaries extending back to about middle of eye; maxillaries toothless in adults (weak teeth in young), but occasionally a few feeble teeth on the anterior part of the lower jaw; vomer and palatines toothless; a well-developed patch of small teeth on the tongue; no basibranchial teeth. Double flap between the nostril openings. Branchiostegals 8–9 + 8–9; gill rakers shorter than in *C. autumnalis*, 12–15 + 21–25. Dorsal fin with 11–13 major rays; 12–14 major anal rays; 14–17 pectoral rays; and 10–12 pelvic rays. Scales large, cycloid, 76–95 pored scales in the lateral line. Vertebrae 62–65; 71–123 pyloric caeca.

Size: The largest known specimen was 36 cm (14 inches) long and weighed about 0.45 kg (1 lb).

Sexual dimorphism: No obvious external differences between sexes. No spawning specimens have been taken, but presumably the males develop lateral spawning tubercles.

Colour: Anadromous adults are brown to green above and bright silver below. The dorsal, adipose, and caudal fins have a dusky tinge, whereas the paired fins and anal fin are usually immaculate. The young are coloured like the adults and have no parr marks.

Distribution

Known certainly only from North America, although probably present also in the Chukotsk and Kamchatka regions of Siberia. (Kurenkov and Stroumov (1965) record a cisco from Kamchatka that appears to be *C. laurettae.*) In North America from Cook Inlet, Gulf of Alaska, north and east as far as Oliktok near the mouth of the Colville River.

Taxonomic Notes

Coregonus laurettae was originally named from specimens from Point Barrow and Port Clarence, Alaska, by T. H. Bean in 1881. The generic name of the Bering cisco is sometimes given as *Leucichthys*; reasons for using the generic name *Coregonus* are given in the introductory notes for the family. In the past, *C. laurettae* and *C. autumnalis* have often been confused, and *C. laurettae* is commonly listed as a synonym of *C. autumnalis.* Recently, McPhail (1966) redefined *C. laurettae,* established its validity as a species, and discussed its relationship to *C. autumnalis.* Another species *Argyrosomus alascanus,* named by N. B. Scofield from Point Hope, Alaska, in 1899 is a synonym of *C. laurettae.*

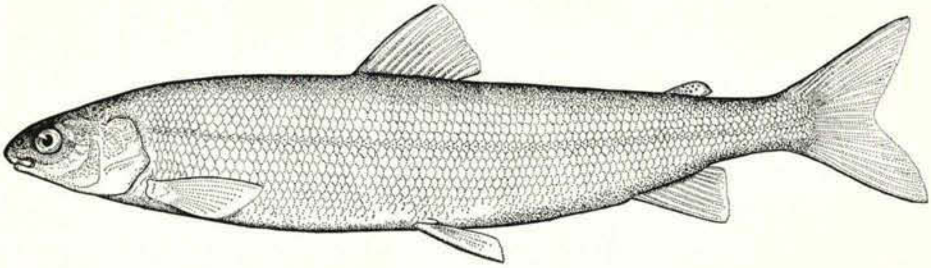
Postglacial Dispersal

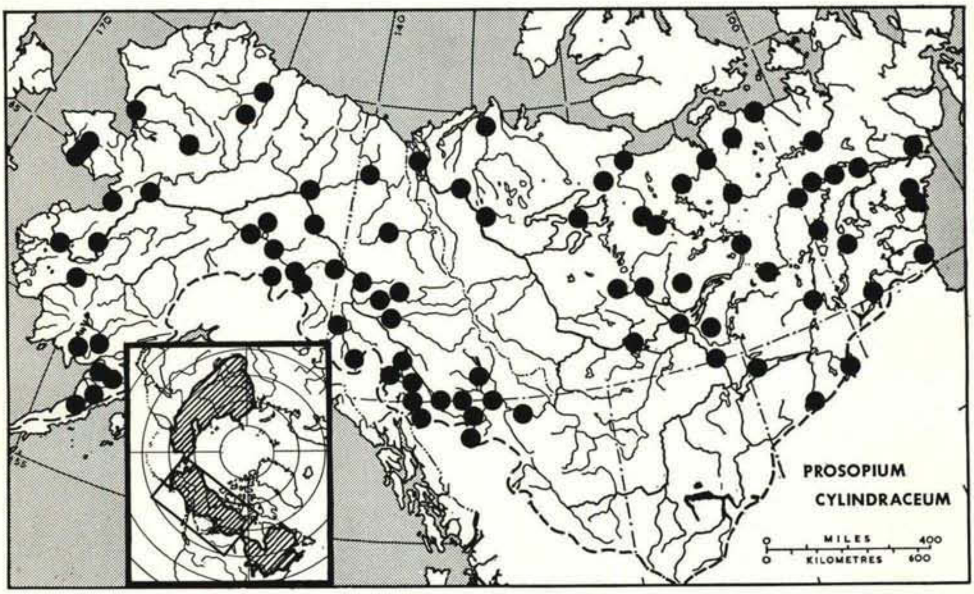
The geographic range of *C. laurettae* is virtually confined to the area of the Bering glacial refuge. This species undoubtedly survived glaciation in the Bering refuge and has not significantly expanded its range postglacially. The record from Cook Inlet suggests there may have been more than one refuge in Alaska.

Biology

Virtually nothing is known about the biology of the Bering cisco. They are most commonly taken near the mouths of rivers and in brackish lagoons. The few stomachs that have been examined indicate that the adults feed mainly on crustaceans (amphipods). Presumably the Bering cisco is anadromous, like the closely related Arctic cisco, and ascends large rivers during the late summer. Spawning probably occurs in early autumn, and is probably followed by a post-spawning downstream migration of the adults. Nothing is known about the age and growth of the species.

The Bering cisco is probably a good food fish and may be used to some extent by natives in the Bering Sea region. However, because of its small size it is not commonly taken in salmon or whitefish nets.




PROSOPIUM
CYLINDRACEUM
0 MILES 400
0 KILOMETRES 600

ROUND WHITEFISH

Prosopium cylindraceum (Pallas)

Prosopium means *a mask*, from the large bones before the eyes, and *cylindraceum* means *like a cylinder*. The French common name for this species is *ménomini rond*.

Distinguishing Characters

Body rounded in cross section; small adipose fin; moderate caudal peduncle with 24–27 rows of scales; small mouth.

Description

Body cigar-shaped, round in cross section; head short, usually more than 4 times into standard length; eye moderate, a little shorter than snout. Adipose eyelid with a ventral notch (Fig. 13). Snout projects beyond lower jaw; profile of upper lip vertical or sloping down and back. Mouth small, no teeth in jaws or mouth except for a few embedded teeth on the tongue. Single flap between the nostril openings (Fig. 14A). Branchiostegals 6–9 + 7–9; gill rakers moderate, 5–8 + 9–13 (usually 6–8 + 10–13 in our area). Dorsal fin with 13–15 major rays; 11–13 major anal rays; 14–17 pectoral rays; and 9–11 pelvic rays. Base of adipose fin usually equal to or (in smaller fish) much less than 1.5 times the eye diameter. Scales large, cycloid, 74–108 pored scales in lateral line; 24–27 horizontal scale rows around the narrowest part of the peduncle. Vertebrae 58–65 (usually 60–65 in our area). Pyloric caeca 61–130 (usually 70–130 in our area).

Size: Fork length up to 50.8 cm (20 inches), and weight up to 2 kg (4.5 lb).

Sexual dimorphism: There are no obvious external differences between sexes except at spawning time. Spawning males have well-developed tubercles in rows along the sides; these are present in females, but are weakly developed.

Colour: Adults are dark brown to olive green above and silvery below. Some specimens have distinct dark spots on the head and adipose fin. Dorsal fin dusky, and the other fins immaculate. Young (up to about 18 cm, or 7 inches) are coloured like the adults but with 7–13 large dark oval parr marks on each side.

Distribution

Siberia and North America. In the USSR, from Bering Strait west along the arctic coast as far as the Yenisei River, and south on Bering Sea drainages to northern Kamchatka, and in northern drainages entering the Sea of Okhotsk. In North America, in Arctic Ocean drainages east to Labrador, and in Bering Sea drainages south to Alaska Peninsula. On the Pacific slope in Kenai Peninsula, Susitna, Copper, Alsek, Chilkat, and Taku drainages. Its occurrence is sporadic towards the southeast, and there is almost or completely a discontinuity in the range near the Manitoba–Ontario boundary. Extending south and east to the Maritimes and New England, and to the Great Lakes other than Lake Erie.

Taxonomic Notes

The first name for the round whitefish, *Salmo cylindraceus,* is attributed to Pallas in Pennant (1784) and was based on Siberian specimens. In North America, Richardson (1823) named *Coregonus quadrilateralis* from Fort Enterprise north of Yellowknife. Richardson's form was later reduced to a subspecies of *cylindraceus,* and Dymond (1943) and Walters (1955) subsequently argued against recognition of subspecies. Reasons for using the genus *Prosopium* rather than *Coregonus* are given in the family introduction. Two other forms named from our area, *Prosopium preblei* Harper and Nichols 1919, and *P. hearnei* Fowler 1948, are apparently indistinguishable from *P. cylindraceum.*

The nearly disjunct North American range of this species apparently corresponds to a separation into two morphological types (see table). Northwestern populations have high mean gill-raker (17.8–19.2) and pyloric caeca (94.1–106.2) counts, whereas southeastern populations have low mean gill-raker (16.0–17.0) and pyloric caeca (67.6–82.8) counts. There is no apparent clinal variation over the range of each form (see table), despite the wide difference in climates encountered. Morphological variation is therefore more probably genetic and related to origin from two long isolated refuges rather than due to present environmental influences.

Variation in gill-raker and pyloric caeca counts in North American *Prosopium cylindraceum.*

	Gill rakers								Pyloric caeca													
	14	15	16	17	18	19	20	21	61–62	66	71	76	81	86	91	96	101	106	111	116	121	126–130
Nome R.				3	3	3	1					1		1	2	2		2		1		
Lower Yukon (below Nulato)				1	3	6	3	1			1		2	1	2	3	2	1		1	1	
Upper Yukon (above Nulato)			3	8	14	8	4				1		1	6	4	2	2	1	2	1		
Bristol Bay drainage			1	2	7	5	1	2				2		4	1	2	3	2	2	1		
Lower Mackenzie (Great Slave L. and below)				1	2	3	2	2						1		1	3	1	1	1	1	1
Upper Mackenzie (above Great Slave L.)				2	4	3	5					1			3		2		2			
Back R.				4	10	6	5	1				1		1	1	2	7	4		2		2
Thelon R.			2	5	7	8	4	2					2	2	1	6	5	2		1	1	
Maguse R.					3	5	3	1				1	2	1	2	1	2	1	2			
Labrador		2	2	4	1				1	3	2	2		1								
Great Lakes	2	18	8	13	5	1			5	6	3	6	6	4		1						
Connecticut R.		2	4	4	2					1	1		1	2								

Postglacial Dispersal

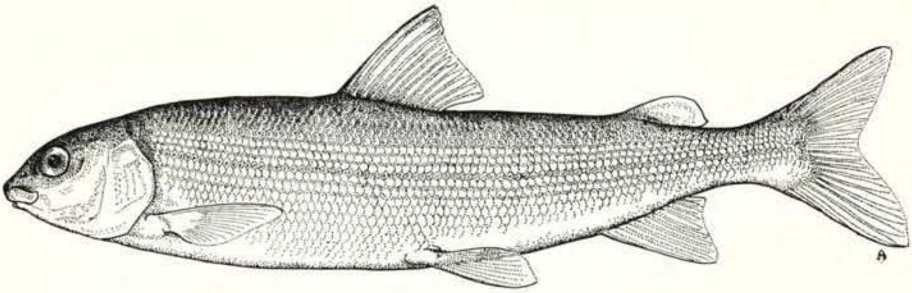
Round whitefish probably survived in at least two North American glacial refuges, one in the southeast, the Mississippi refuge (from which they spread northward into Ontario and Quebec), and another in the Bering region (from which they spread east as far as the northwestern shore of Hudson Bay). Their tolerance of brackish water, periglacial conditions, and swift running water has evidently helped them cross watershed boundaries, especially during glacial retreat. Thus they are widespread in all the Pacific coastal drainages from the Susitna south to the Taku rivers, each of which they must have invaded either during interchange of mountain headwaters or by moving from river mouth to river mouth through temporary brackish water "bridges." Their absence from the Nelson River drainage, and scarcity in the Churchill system (so far being recorded only from the vicinity of Reindeer Lake, and at the Churchill River mouth) is as yet unexplained. Even in southern areas where they do occur, their distribution is sporadic, suggesting that they may have stringent ecological requirements. In western North America their southward spread may have been checked by the closely related *Prosopium williamsoni*, whose range they scarcely overlap.

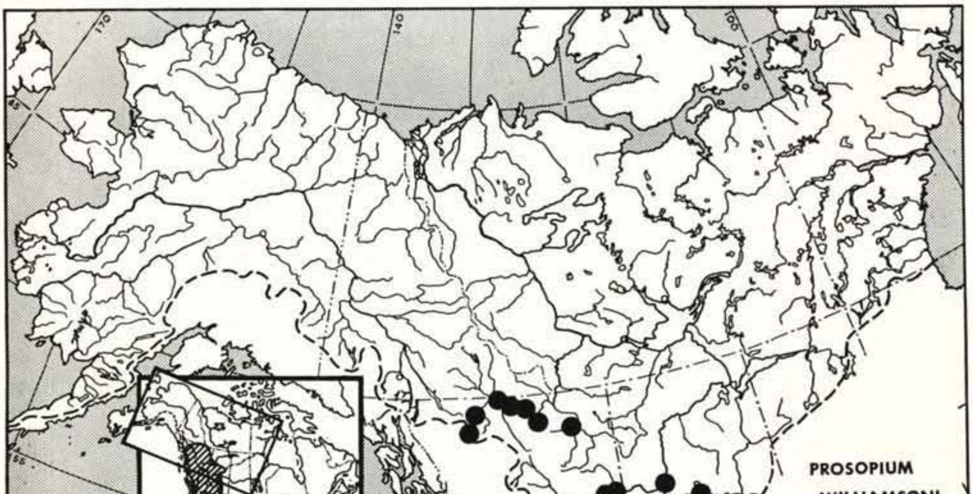
Biology

The round whitefish is one of the most widespread and common species in northern waters, although its distribution is sporadic towards the south. It is most abundant in shallow areas of lakes and in clear streams, and has been reported in brackish waters off the Mackenzie, Coppermine, and Churchill rivers and off Clearwater (in Quebec). It feeds in shallows and inshore. In several northern lakes stomachs have contained caddis larvae and pupae, chironomid larvae, and small gastropods. Specimens from Artillery Lake had eaten large quantities of Cladocera (Rawson, 1951). Round whitefish are frequently reported to feed heavily on the eggs of other species, including chum salmon, lake trout, and suckers. Harper (1961) recalls that in New England the round whitefish were called "shad-waiters" because they met and "waited upon" the spawning shad in order to devour their eggs; he adds that in Ungava round whitefish play the role of "sucker-waiters."

In Great Slave Lake round whitefish have an average fork length of 31.2 cm (12.3 inches) when aged 5 years, and 44.7 cm (17.6 inches) at age 10; the oldest recorded fish was 14 years old (Rawson, 1951). In Great Bear Lake most fish mature in their 6th or 7th year (Kennedy, 1949). Spawning occurs in autumn along the shores of lakes or in streams. Harper (1948) reports an upstream spawning migration in late October in the Northwest Territories. Eggs are shed over gravel, evidently without any nest construction or parental care. Large females may lay up to 20,000 eggs.

In Siberia round whitefish are of some commercial importance, but in our area they do not usually occur in sufficient numbers for commercial exploitation. In the Great Lakes region they are said to be an excellent food fish (Koelz, 1929).




PROSOPIUM
WILLIAMSONI
MILES 400
KILOMETRES 600

MOUNTAIN WHITEFISH

Prosopium williamsoni (Girard)

Williamsoni is named after Lieut. R. S. Williamson of the U.S. Pacific Railroad exploration. The French common name for this species is *ménomini des montagnes.*

Distinguishing Characters

Body rounded in cross section; large adipose fin; narrow caudal peduncle; small mouth.

Description

Body cigar-shaped, somewhat compressed in adults and round in young fishes; head short, more than 4 times into standard length; eye moderate, a little shorter than snout. Adipose eyelid with a ventral notch (Fig. 13). Snout projects beyond lower jaw; profile of upper lip vertical or sloping down and back. Occasional individuals have the snout prolonged and slightly upturned. Caudal peduncle slender. Mouth small; no teeth in jaws or in mouth except for a few embedded teeth on the tongue. Single flap between the nostril openings. Branchiostegals 7–10 + 7–10; gill rakers moderate, 8–11 + 11–15 (usually 8–10 + 11–13 in our area). Dorsal fin with 11–15 major rays; 10–13 major anal rays; 14–18 pectoral rays; and 10–12 pelvic rays. Adipose fin large, its base more than 1.5 times the eye diameter (except in very young fish). Scales large, cycloid, 75–89 pored scales in lateral line; 20–23 (rarely 24) horizontal scale rows around the peduncle. Vertebrae 53–61 (usually 57–60 in our area). Pyloric caeca 50–146.

Size: Total length rarely up to 57 cm (22.5 inches), usually much smaller; weight up to 2.3 kg (5 lb) (a 48-cm (19-inch) specimen was angled by Orville Welch from Athabasca River in June 1963).

Sexual dimorphism: There are no obvious external differences between sexes except at spawning time. There are well-developed white tubercles in 8–10 rows along the sides of spawning males; in females these tubercles are present but are only weakly developed.

Colour: Adults are dark brown to olive green above and silvery below. The scales on the back are often outlined in dark pigment. Dorsal fin usually dusky; the other fins are immaculate. Young (up to about 12 cm, or 5 inches) coloured like adults, but with 7–11 large oval parr marks along lateral line.

Distribution

Found only in western North America, from interior drainages in Nevada, and the upper Colorado system, north to the Stikine and Liard rivers. In our area, known only from Mackenzie River headwaters, in the upper Liard, and in the Peace downstream as far as Peace River townsite and in the Athabasca River downstream as far as Athabasca townsite.

Taxonomic Notes

The mountain whitefish was described as *Coregonus williamsoni* by Girard in 1856 from Oregon. Reasons given by Norden (1961) for placing this species in the genus *Prosopium* are outlined in the introductory notes for the family. *Prosopium oregonium,* reported to occur in Lesser Slave Lake as well as in Oregon, has been shown by Holt (1960) to be indistinguishable from *P. williamsoni.* A subspecies *cismontanus* has been named for populations east of the Continental Divide, but no consistent character differences have been shown. A variant form with long, pointed, and upturned snout occurs sporadically among collections of whitefish with normal snouts; its significance is unknown.

Prosopium williamsoni is a mountain form closely related to the more widely ranging *P. cylindraceum.* The two species probably evolved while geographically isolated, but their ranges now overlap in a few places such as Dease Lake and the Liard River. There is no evidence of interbreeding. The mechanisms enabling these similar species to occur together without either fusion or displacement of the less successful through competition are as yet unknown.

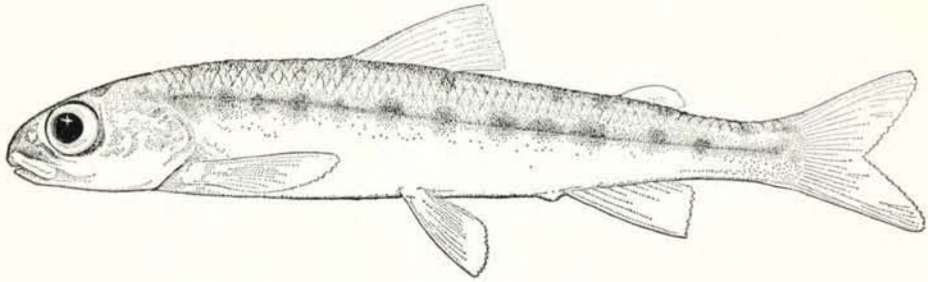
Postglacial Dispersal

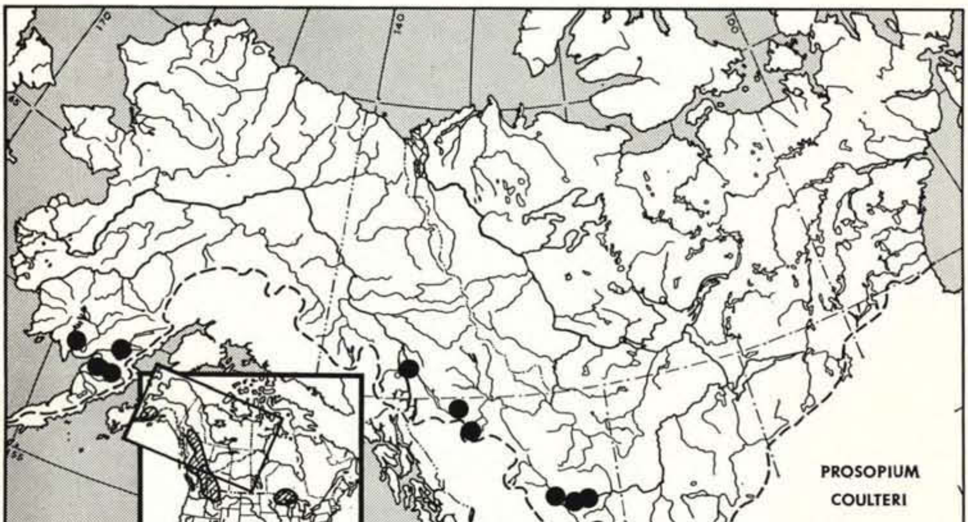
The mountain whitefish survived the last glaciation south of the ice sheet in western North America, either on one or both sides of the Continental Divide. Its distribution suggests that it may have crossed the Divide, in either direction, more than once. Alterations in drainage pattern are relatively common in the type of unstable and mountainous headwater area frequented by mountain whitefish. Watershed boundaries are therefore less likely to impose limits on this than on lowland species. The fact that the ranges of *P. williamsoni* and *P. cylindraceum* are almost (although not quite) mutually exclusive suggests that competition may possibly limit the range of each to the habitat to which it is best suited.

Biology

Mountain whitefish occur in both lakes and streams, sometimes in quite fast water, either clear or silty. In northern lakes they are taken only in shallower waters, down to about 10 m (30 ft). They feed mainly on bottom organisms, including midge, mayfly, stonefly, and caddis larvae (McHugh, 1940; Godfrey, 1955; McCart, 1965), but in waters poor in bottom fauna they may feed at any level including the surface. Fish that had completed nine winters growth were 19.7 cm (7.8 inches) in standard length in Bow River, and 36.6 cm (14.4 inches) in Cultus Lake (McHugh, 1940). The oldest recorded fish was 18 years of age. Sexual maturity is reached in 3 or 4 years. Kootenay Lake seems to contain two or more "races" that may differ morphologically, and that spawn at different times and places, varying from late October to early February. In other British Columbia areas spawning is reported to be from November to January. Eggs are laid over gravel, usually in streams but sometimes on gravel shoals along the lake edge. In Kootenay Lake spawning takes place only in darkness, and the same has been observed in Montana. No nests are constructed. In Nicola Lake, B.C., females of 28.2 cm fork length laid an average of 3570 eggs with mean diameter of 2.8 mm (J. W. Cartwright, personal communication). Eggs probably hatch in early spring, and fry are found along the edges of streams and in backwaters for several weeks after hatching.

Mountain whitefish will take an artificial fly, and are quite game, as well as tasty. Angling for them is on the increase in western Canada. Late autumn and winter fishing for "grayling," as the mountain whitefish is often wrongly named, is popular in the Kootenay region. Conservation Officer J. D. Williams of Fernie reports checking two anglers who had together taken nearly 500 fish in 1 day. He adds "One of the local anglers, commonly known as Grayling Bill Peters, must have a rather strong stomach. His method of keeping his 'scratchers' (stone-fly larvae) from freezing and also having them handy for use is to keep them under the lower lip." This method of carrying scratchers is to be recommended, as it keeps them not only unfrozen but highly active. Other baits in use include salmon eggs, maggots, and canned corn. The hook used must be small. The world's record mountain whitefish, angled by Conservation Officer R. A. Rutherglen from the Lardeau River, B.C., in 1959, was 22.5 inches in total length and weighed 4 lb 7 oz.




PROSOPIUM
COULTERI
MILES
KILOMETRES

PYGMY WHITEFISH

Prosopium coulteri (Eigenmann and Eigenmann)

Coulteri is named after Dr J. M. Coulter, a botanist. The French common name for this species is *ménomini pygmée*.

Distinguishing Characters

Body rounded in cross section; blunt head; small toothless mouth; large eye; small adipose fin; large scales.

Description

Body cigar-shaped, round in cross section; head short, usually more than 4 times into standard length; eye moderate, a little shorter than snout. Adipose eyelid with a ventral notch (Fig. 13). Snout blunt, its tip slightly ahead of tip of lower jaw; profiles of upper lip vertical or sloping down and back. Mouth small; no teeth in jaws or mouth except for a few embedded teeth on the tongue. Single flap between the nostril openings. Branchiostegals 6–9 + 6–9; gill rakers moderate 3–7 + 8–13. Dorsal fin with 10–13 major rays; 10–14 major anal rays; 13–18 pectoral rays; and 9–11 pelvic rays. Scales large, cycloid, 50–70 pored scales in lateral line. Vertebrae 50–55. Pyloric caeca 13–33.

Size: Usually under 15 cm (6 inches) but in some lakes up to almost 28 cm (11 inches).

Sexual dimorphism: There are no obvious differences between sexes except at spawning time. Spawning males have well-developed tubercles in rows along the sides above the lateral line, on top of the head, and on the paired fins. These tubercles are also present in females, but are only weakly developed.

Colour: Adults are dark brown above and silvery below. All fins are usually immaculate. Young and adults, less than 5 inches long, have 7–14 oval parr marks along lateral line. These are indistinct, or absent, on larger fish.

Distribution

Found only in North America. The distribution is disjunct: in the west in the Columbia system in Washington, Montana, and British Columbia, in the Fraser, Skeena, and Alsek river systems; in the headwaters of the Yukon River, and in the Bristol Bay region of Alaska; also in the east in Lake Superior. In our area it is recorded from the Peace, Liard, and upper Yukon river systems, and several lakes in the Bristol Bay area.

Taxonomic Notes

The pygmy whitefish was first described as *Coregonus coulteri* by Eigenmann and Eigenmann in 1892 from the Kicking Horse River at Field, B.C. Reasons given by Norden (1961) for placing this species in the genus *Prosopium* are outlined in the introductory notes for the family. There are no synonyms for this well-marked species, and superficially its taxonomy is unusually simple for a whitefish. Unfortunately, this simplicity is probably only a reflection of our ignorance. In Aleknagik Lake and other large lakes in the Bristol Bay region of Alaska the pygmy whitefish occurs sympatrically with the round whitefish, *P. cylindraceum,* and also with a third form of *Prosopium* that is intermediate between *P. cylindraceum* and *P. coulteri* in the number of lateral line scales and vertebrae. Because it is intermediate in some characters this third form could be a hybrid between *P. coulteri* and *P. cylindraceum.* However, in nearby Chignik Lake only *P. coulteri* and the intermediate form occur, and *P. cylindraceum* is totally absent. Possibly this form represents an undescribed species. In Aleknagik Lake the intermediate form is more abundant than the pygmy whitefish, and apparently differs from both *P. coulteri* and *P. cylindraceum* in its ecology. The intermediate form is found most abundantly in shallow water near the outlet of the lake, whereas *P. coulteri* is found mainly in deep water, and *P. cylindraceum* in both deep and shallow water. The problem of the relationship between this intermediate form and *P. coulteri* is being studied by P. McCart (personal communication).

Postglacial Dispersal

The distribution of the pygmy whitefish indicates that it survived glaciation in several refuges. Presence of the species in Lake Superior suggests survival in a Mississippi refuge, but its absence from such large lakes as Nipigon, Wollaston, Reindeer, Athabasca, Great Slave, and Great Bear, is strange. Its ecology suggests that it was ideally suited to take advantage of the series of large proglacial lakes that were formed in central Canada during the retreat of the glaciers. Perhaps *P. coulteri* is present in some of these lakes and simply has not been collected. It was not until 1952 when bottom trawls were used at depths greater than 10 fath that the pygmy whitefish was taken in Lake Superior.

The distribution of *P. coulteri* in western North America extends from near the southern limits of glaciation northward to the unglaciated Bristol Bay region of Alaska. Most of this distribution lies within glaciated areas and was probably attained primarily through northward dispersal from a refuge in the Columbia system. At least some of the populations around Bristol Bay probably represent a distinct form that survived glaciation in that area.

Biology

The pygmy whitefish is most abundant in the lakes, rivers, and streams of mountainous areas. It is taken both in moderate-sized and large lakes, and in silty and clear streams. In rivers and streams it is usually found in moderate to swift water. In lakes it is most commonly taken in water deeper than 20 ft, but has been taken in shallows only a few feet deep. Little is known about its behaviour. The pygmy whitefish is carnivorous and feeds mainly on bottom organisms (particularly aquatic insect larvae, crustaceans, and small molluscs). In Lake Superior ostracods and *Pontoporeia* (an amphipod) are the main foods. In British Columbia, pygmy white-fish mature in their 2nd or 3rd year, and may live up to 9 years (McCart, 1965). In Lake Superior the maximum age recorded is 8 years (Eschmeyer and Bailey, 1955). In most areas growth is very slow (fish in their 8th year from Lake Superior were only 137 mm (5.4 inches) long), but in Maclure Lake near Smithers, B.C., pygmy white-fish grow up to 272 mm (10.7 inches) in a comparable time.

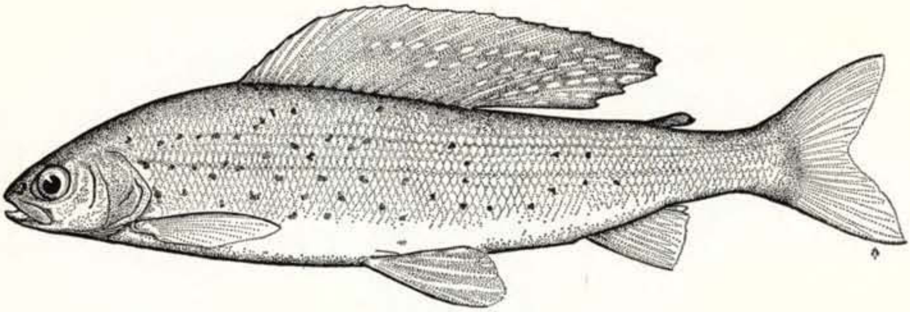
Nothing is recorded about the spawning habits of this species. Spawning has been recorded in the late summer, autumn, or early winter depending on the area. Apparently spawning takes place either in streams or lakes. As in other members of the genus, the eggs are probably simply scattered over gravel areas. The eggs probably develop over winter and hatch in the early spring. A large female can lay up to 600 eggs. The mature eggs are about 2 mm in diameter.

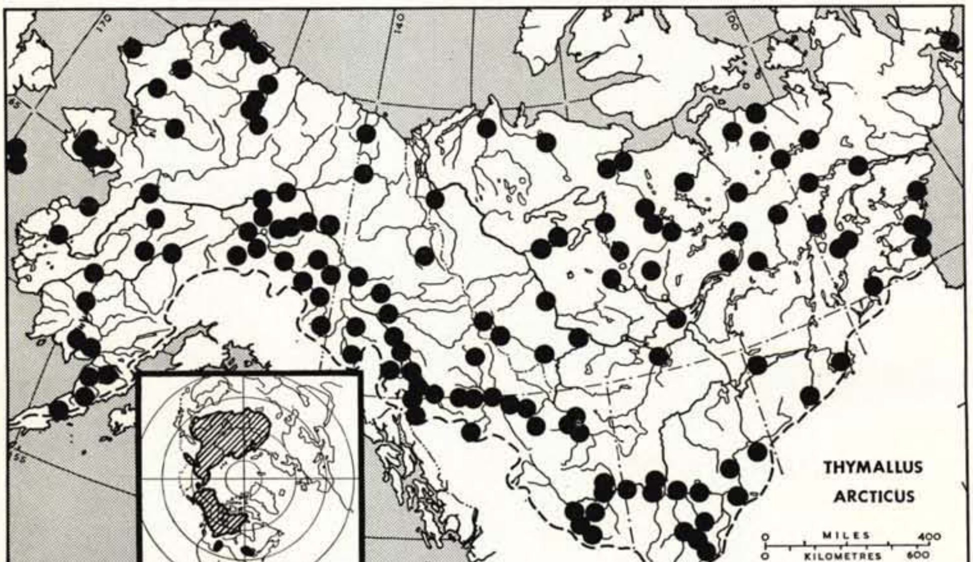
Pygmy whitefish are of no direct commercial importance, but serve as forage for such larger predaceous species as Dolly Varden and Arctic char.

Arctic grayling. Photo: C. C. Lindsey.

THE GRAYLINGS — Family THYMALLIDAE

The graylings are troutlike fishes with rather small but toothed jaws, large scales, and a large and often colourful flaglike dorsal fin. They frequent streams and cold lakes in northern North America, USSR, and Europe, including Great Britain. Several Old World species are recognized, but only one in North America. Some authors place the graylings, as well as the whitefish, with the trout in the family Salmonidae.





THYMALLUS
ARCTICUS
MILES
400
KILOMETRES
600

ARCTIC GRAYLING

Thymallus arcticus (Pallas)

Thymallus refers to the supposed odour of wild thyme and *arcticus* means *of the arctic.* The French common name for this species is *omble arctique.*

Distinguishing Characters

The greatly enlarged dorsal fin, and the small mouth with teeth in both jaws.

Description

Body elongate, compressed; head short, about one-quarter standard length; eye large, about equal to snout. Mouth moderate with small teeth in both jaws and on the tongue, head of vomer, and palatines; no basibranchial teeth. Branchiostegals 8–9 + 8–9; gill rakers moderately developed, 5–7 + 11–15. Dorsal fin greatly enlarged, with a total of 19–24 rays, its base equal to or longer than the head except in very small fish; 11–14 anal rays; 14–16 pectoral rays; and 10 or 11 pelvic rays. Caudal fin deeply forked, the lower lobe sometimes slightly longer than the upper. Scales large, cycloid, 77–98 pored scales in lateral line. Vertebrae 58–61. Pyloric caeca 14–21.

Size: Length to 61 cm (24 inches) and weight to 2.3 kg (5 lb). The angling record is for a 53-cm (21-inch) grayling weighing 2.5 kilo (5 lb 7 oz) from Great Bear Lake.

Sexual dimorphism: During spawning, males are more vividly coloured than females. In mature males the dorsal fin, if depressed, extends back to or beyond the adipose fin, and the pelvic fins almost reach the anus. In mature females the dorsal and pelvic fins are much shorter.

Colour: In adults the back is dark purple or blue, the sides are grey with scattered black spots (more numerous in young specimens). A distinct dusky stripe runs from below the pectoral fins to the pelvic fins, and a black stripe marks the inner edge of the lower jaw. The dorsal fin is dark with rows of orange spots and a few emerald green spots, and is edged with red or orange. On the pelvic fins there are longitudinal orange stripes bordered with black. The colours are more intense in males than in females. Young specimens have 10–19 narrow dark parr marks along the lateral line plus 2 or 3 irregular rows of spots above these.

Distribution

In Eurasia, in Arctic Ocean drainages from the Kara and Ob rivers east to Chukotsk Peninsula, south to northern Mongolia, and south on Pacific Ocean drainages in Asia to the upper Yalu River. Taken in salt water in Kara Bay. In lakes on St. Lawrence Island in Bering Sea. In North America, throughout Bering Sea and Arctic Ocean drainages east to Vansittart Island off Melville Peninsula (but not otherwise recorded from Canadian Arctic islands) and south on the west coast of Hudson Bay to Owl River south of Churchill. In northern Saskatchewan, Rawson (1950) writes that grayling are widespread in the Athabasca system, and general in the Reindeer Lake area, but doubtful in the remainder of the Churchill River drainage of that province. On the Pacific coast, in the Susitna, Copper, Alsek, Taku, and Stikine rivers. In the headwaters of the Missouri River some grayling occurred upstream from Great Falls, Montana. Their native range in this region has been greatly modified through extinctions, hatchery plantings, and introduction of Canadian stocks. In Michigan, grayling occurred at one time but were exterminated by man's activities.

Taxonomic Notes

Pallas named the Arctic grayling of the Ob River in Siberia as *Salmo arcticus* in 1776. It was subsequently placed in the same genus as *Thymallus thymallus* of Europe. In North America Richardson named the grayling from Winter Lake (150 miles north of Yellowknife) as *Thymallus signifer* in 1823. Walters (1955) showed that this form did not differ significantly from the Russian forms *T. arcticus pallasi* and *T. a. grubei* natio *mertensi*; therefore, because Richardson's name has priority, Walters concluded that the North American and Siberian forms should all be in the subspecies *Thymallus arcticus signifer*. We choose not to recognize subspecies at all within *T. arcticus* unless further evidence warrants them; possibly the form *T. a. baicalensis* in Lake Baikal should be recognized, but the only distinctive character given by Berg (1948–49), the short dorsal fin, is one varying widely even in our area. The New World forms *T. tricolor* from Michigan and *T. montanus* from Montana have not been shown to differ from *T. arcticus*. Valenciennes named *Thymallus ontariensis* in 1848 from a specimen said to have been brought from Lake Ontario, but this was probably a mislabelled European specimen (Jordan and Evermann, 1896, p. 2870). A careful study of the osteology of *Thymallus* is given by Norden (1961).

Postglacial Dispersal

The North American range of the Arctic grayling includes two unglaciated areas, the Bering and Mississippi refuges. Presence of grayling on St. Lawrence

Island (a remnant of the Bering land bridge), as well as in Montana and Michigan, indicates that *T. arcticus* occupied both refuges during the last glaciation.

It is difficult to understand why southern grayling did not expand northward after the ice retreat. Possibly they did, and were later extirpated from the intervening zone, which later separated their northern and southern ranges, during the warm postglacial "hypsithermal" period. However, climatic conditions sufficiently warm to eradicate grayling from the whole of southern Canada might be expected also to have eradicated them from Michigan, even if not from the higher elevations in Montana.

F. M. Atton has drawn to our attention that lateral line scale counts are lower in Mackenzie River grayling than in grayling from either the Yukon River or the Barren Grounds. Possibly grayling did invade the Mackenzie system from the south, and northern populations are in fact derived from two sources. Morphological and physiological studies are needed, although these may be hampered by the difficulty of finding "pure" stocks of southern grayling.

Biology

Arctic grayling are characteristically found in schools in clear water, throughout most lakes and streams of the north. They may also be taken at several points along the Mackenzie and Yukon rivers, but usually where clear tributaries enter. In the large lakes they are generally close to shore, along rocky shores, and near stream mouths. Miller (1946) writes, of the outlet of Great Bear Lake, "During August the grayling played and leaped here constantly. Literally hundreds were in the air at one time, surrounded by flocks of frustrated gulls futilely endeavouring to catch them and plunging first at one splash then another, in a sort of frenzy." We investigated local reports of "freshwater flying fish" in Crystal Lake near Mayo, Y.T., and found these to be based on enormous numbers of dwarfed grayling, which covered the lake surface with rises in the manner described by Miller.

Food studies on several northern lakes indicate that terrestrial insects form the most important summer food of grayling, often comprising over half of the diet. However, grayling are opportunistic feeders; some fish from Great Slave Lake were gorged with amphipods (Rawson, 1951), and shortly after ice break-up, when little terrestrial food is available, caddis and mayfly nymphs may be taken from the bottom (Rawson, 1950). Cladocera, snails, small fish, and even young lemmings have been recorded in grayling stomachs. On the Seward Peninsula, Alaska, we have taken grayling that had eaten ninespine sticklebacks. At Andreafsky on the Yukon River, grayling were seen being chased by chum salmon, in a small creek where the grayling were probably eating salmon eggs.

Grayling in their 6th summer had average fork lengths of 43.1 cm (17 inches) in Reindeer Lake, 40.5 cm (15.9 inches) in Great Slave Lake, and 35.6 cm (14 inches) in Great Bear Lake. In the latter water most grayling mature in their 5th summer, and may survive to their 12th (in contrast to Montana grayling that reach early maturity and most of which die after their 4th summer).

In our area grayling spawn from early May to mid-June, at about the time that lake ice cover is breaking, usually in small streams over a gravel or rocky bottom.

Spawners in the outlet of Reindeer Lake mostly yielded between 4000 and 7000 eggs per female, with a few of the largest fish containing over 10,000 eggs (Rawson, 1950). Eggs when laid are amber coloured, heavy, slightly adhesive, and 2.5 mm in diameter. They are apparently shed over the bottom without construction of a redd or any parental care. However, Fabricius and Gustafson (1955) have described spawning in the European grayling *Thymallus thymallus,* in which species the eggs are spawned below the surface of the gravel. Young hatch within 16–18 days at temperatures near 9 C. Detailed observations on the spawning of *T. arcticus* are sorely needed.

Arctic grayling often swim in midstream a short distance below the surface, periodically rising to take surface food. They are readily caught on a dry fly or indeed on any small lure. As a pan fish they are first-rate if cooked as soon as caught. They are very vulnerable when congregated in small streams at spawning time. Indians at Great Bear Lake report that grayling spawn in small tributaries in early spring, and then descend in mid-June to larger rivers and to bays of the lake; during this downstream migration they are sometimes taken in specially constructed traps, and used largely for dog food (Miller, 1947).

The Arctic grayling is a uniquely attractive fish, beautiful to look at, sporting to catch, and quite palatable. The iridescent peacock colouration of the male in spawning dress defies description. The Arctic grayling is sensitively balanced to its environment, and cannot cope well with man's encroachment. In streams of northern Michigan grayling were once abundant, but had been totally exterminated by the late 1930's. Logging operations, pollution, introduction of foreign competitors such as brown trout, and overfishing, may all have contributed. Arctic grayling still abound in many parts of our area, but their slow growth and ease of capture make them susceptible to local extirpation, especially in such exposed sites as streams bordering the Alaska Highway.

Concerning the supposed odour of thyme, which is said to be the reason for the name *Thymallus,* D'Arcy Thompson (1946) writes: "The odour of thyme is not perceptible in British grayling, and naturalists elsewhere have failed to perceive it." Sir D'Arcy quotes several learned authorities on the matter, and concludes: "For my part I think the odour was imagined by the grammarians to account for the name."

THE TROUTS, CHARS, AND SALMONS—
Family SALMONIDAE

The family Salmonidae is considered by some authorities to include the whitefishes and graylings as well as the trouts, chars, and salmons. Although these fish share common characters, the family Salmonidae is here restricted to the species in our area with strong teeth in the jaws, small scales, and a short or moderate soft dorsal fin. Many are anadromous, spending much of their lives in the sea but always returning to fresh water to spawn. The eggs are large, yellowish or pinkish, and nonadhesive, and in most species are laid in shallow depressions or "redds" constructed in gravel-bottomed streams. In our area all species of *Salvelinus* and *Oncorhynchus* spawn in autumn, whereas native *Salmo* spawns in spring. Because they are large and highly edible, the salmonids are of great importance to man in many parts of our area, both as commercial human or dog food and also, increasingly, as sport fish.

The natural range of the family Salmonidae covers cool portions of the northern hemisphere. (They have been introduced successfully into the temperate southern hemisphere.) There are five genera (two, *Brachymystax* and *Hucho,* are confined to Eurasia), and roughly 30 species. The Pacific salmons *Oncorhynchus* have evolved in the North Pacific region, and have only a restricted distribution in arctic waters. The trouts *Salmo* are adapted to more southerly waters than are the chars *Salvelinus*; only one native species of *Salmo* ventures into our area, whereas chars are widespread. Of the latter, the lake "trout" *Salvelinus namaycush* is very distinctive; hence the name *Cristivomer namaycush* of some writers. The other chars are taxonomically confusing; like the whitefishes, they are adapted to life around glacial margins, and have undergone comparable isolations and recombinations, as well as modifications by the local environment. For these reasons *Salvelinus malma* and *S. alpinus* cannot be distinguished in the key without reference to the locality from which the specimens were taken.

Young adult salmonids are very different in appearance, and are served here by separate keys. Sea-run fish of all species may also be hard to identify due to a layer of silvery guanine that obscures the body markings.

KEY TO SALMONIDS OVER 13 CM (5 INCHES) LONG

1(14) 8–12 major rays in the anal fin 2

2(9) Spots dark brown or black on light background; teeth on head and shaft of vomer, forming a strip down the centre of the roof of the mouth several times as long as it is wide (Fig. 18A) .. 3

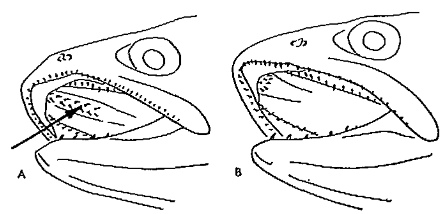


Fig. 18. A, Head of *Salmo clarki*, with well-developed teeth along the shaft of the vomer; B, head of *Salvelinus alpinus*, with teeth on vomer only at the front.

3(4) Large black spots, many surrounded by pale halos; usually a series of pale or reddish spots along the lateral line .... Brown trout, *Salmo trutta* Linnaeus

Brown trout have a square tail, scarcely forked, with few or no spots on it; the adipose is often orange or with orange and black spots; the maxilla extends well behind the eye. Brown trout were introduced from Europe. In our area they have been planted only in the Athabasca and McLeod rivers (upper Mackenzie system); they are not discussed further in this Bulletin.

4(3) No halos around black body spots; generally no pale spots along the lateral line 5

5(6) Red or orange hyoid slashes in parallel grooves on the underside of lower jaw; usually a few teeth behind the tongue between the gills .... Cutthroat trout, *Salmo clarki* Richardson

Cutthroat trout have no distinctive light margins on the fins; the belly is sometimes red in ripe fish, but there is no broad red band on the side; the snout is pointed and the maxilla reaches behind the hind margin of the eye. The coastal cutthroat trout (*S. c. clarki*) ranges along the Pacific coast from California north; it does not occur in our area, but has been reported as far north as Prince William Sound in Alaska. The Yellowstone cutthroat trout (*S. c. lewisi*) occupies the upper Missouri, Columbia, Fraser, and Saskatchewan rivers. It was introduced into McLean Lake near Whitehorse in 1946. Rainbow trout were stocked in the same lake earlier and the two species apparently hybridized. In 1960 McLean Lake was poisoned and in 1961 restocked with rainbow trout from British Columbia.

6(5) Red or orange hyoid slash usually absent from underside of lower jaw (rainbow trout from the Kuskokwim system have a fairly well-developed red slash, and some from the upper Peace a faint and irregular one); never any teeth behind the tongue 7

7(8) Teeth on shaft of vomer few, poorly developed, and deciduous; caudal fin usually unspotted, never with regular rows of black spots; adipose fin without a black margin. No lateral red band on spawning adults .... Atlantic salmon, *Salmo salar* Linnaeus

Occurs on both sides of the North Atlantic. Not recorded from our area, but present in Ungava Bay and southern Greenland.

8(7) Teeth on shaft of vomer well developed, not deciduous; caudal fin distinctly marked with radiating rows of black spots; adipose fin bordered by black spots or a continuous black band; well-developed lateral red band on spawning adults ....
.... Rainbow trout, *Salmo gairdneri* Richardson (p. 159)

In our area native only to the southern Bristol Bay region of Alaska and the upper Mackenzie system. Some introductions of this species have been made in Yukon Territory and the Fairbanks area of Alaska.

9(2) Spots light (red, pink, orange, yellow, or grey) on a dark background; teeth on head of vomer only, in a patch at the front of the mouth not much longer than it is wide (Fig. 18B) 10

10(11) Dark green marbling (wavy markings) always present on back and particularly on dorsal fin ....
.... Brook trout, *Salvelinus fontinalis* (Mitchill) (p. 155)

Native populations not recorded from our area, but known from northern Manitoba close to our southern boundary. Introduced in the upper Mackenzie system (Athabasca and McLeod rivers) and in southeastern Alaska.

11(10) Dark green marbling usually absent from back and never present on dorsal fin 12

12(13) Caudal fin deeply forked (shortest caudal ray less than half longest ray); numerous irregular whitish spots on back and sides; about 90–200 pyloric caeca ....
.... Lake trout, *Salvelinus namaycush* (Walbaum) (p. 137)

13(12) Caudal fin not deeply forked (shortest caudal ray more than half longest ray); regular red, pink, orange, or yellow spots on back and sides; 13–74 pyloric caeca ....
Dolly Varden and Arctic char, *Salvelinus malma* (Walbaum) and
.... *Salvelinus alpinus* (Linnaeus) (p. 149 and p. 143)

—In the Bristol Bay region of Alaska the Arctic char (*S. alpinus*) and the Dolly Varden (*S. malma*) occur sympatrically. *Salvelinus alpinus* has 12–17 gill rakers on the lower limb (usually 14 or 15) and 29–74 pyloric caeca (usually a population mean of 42–50), and *S. malma* has 11–14 gill rakers on the lower limb (usually 12 or 13) and 21–36 pyloric caeca (usually a population mean of about 27).

—In Alaska north of Bristol Bay *S. alpinus* and *S. malma* also occur sympatrically. In this area *S. alpinus* populations have a mean vertebral count of about 66 and a mean lateral pore count over 134, whereas *S. malma* populations have a mean vertebral count of about 68 and a mean lateral pore count of 130 or less.

13(12) — In the upper Yukon and Mackenzie river systems only *S. malma* occurs. In this area *S. malma* has 8–12 gill rakers on the lower limb of the first gill arch.

— Along the arctic coasts of Alaska and Canada west of the Mackenzie Delta only *S. alpinus* occurs (gill rakers 12–15 on lower limb, usually a mean of about 13).

— Along the arctic coast of Canada east of the Mackenzie system, in the Arctic Archipelago, and in Hudson Bay only *S. alpinus* occurs (gill rakers 13–18 on lower limb, usually a mean of about 16).

14(1) 13–19 (rarely 12) major rays in the anal fin 15

15(20) Distinct black spots on back and caudal fin 16

16(17) Spots on tail and back oblong, the longest as long as the vertical eye diameter; posterior adipose eyelid well developed, extending half way to posterior margin of pupil .... Pink salmon, *Oncorhynchus gorbuscha* (Walbaum) (p. 183)

17(16) Spots on tail and back small and irregular, the largest much smaller than vertical eye diameter; posterior adipose eyelid poorly developed, not extending half way to pupil 18

18(19) Flesh along base of teeth in lower jaw black; small black spots on both lobes of tail .... Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum) .... (p. 175)

19(18) Flesh along base of teeth in lower jaw not black; spots on tail absent, or present only on the upper lobe of tail .... Coho salmon, *Oncorhynchus kisutch* (Walbaum) (p. 171)

20(15) No distinct black spots on tail or back, although fine black speckling is common 21

21(22) Gill rakers short, stout, and widely spaced, 19–26 on first gill arch .... Chum salmon, *Oncorhynchus keta* (Walbaum) (p. 179)

22(21) Gill rakers long, slender, and closely spaced, 30–40 on first gill arch .... Sockeye salmon, *Oncorhynchus nerka* (Walbaum) (p. 165)

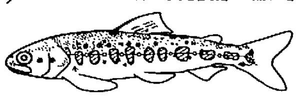
KEY TO YOUNG SALMONIDS 5–13 CM (2–5 INCHES) LONG

1(14) Major rays in anal fin 8–12 2

2(11) Dorsal fin with distinct dark spots, or with first dorsal ray black 3

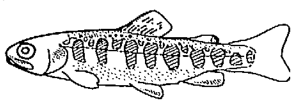
3(8) Coloured spots (red or yellow) on lateral line between or on parr marks (may be missing in hatchery-reared fish and in preserved specimens); combined width of dark areas along lateral line about equal to or greater than width of light areas 4

4(5) Pectoral fins long, as long as depressed dorsal fin; caudal fin deeply forked, the centre rays about half the length of the longest .... Atlantic salmon, *Salmo salar*

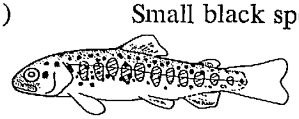


5(4) Pectoral fins shorter than depressed dorsal fin; caudal fin not deeply forked, the centre rays definitely more than half the length of the longest 6

6(7) No definite dark spots other than the parr marks below the lateral line; 8 or 9 wide parr marks, the widest about equal to the eye diameter .... Brook trout, *Salvelinus fontinalis* (p. 155)

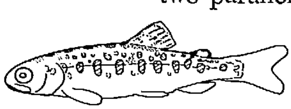


7(6) Small black spots above and below the lateral line in addition to the parr marks; about 11 parr marks, none as wide as the eye diameter .... Brown trout, *Salmo trutta*

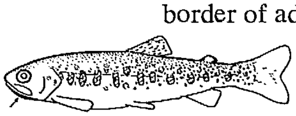


8(3) No coloured (red or yellow) spots; width of dark areas along lateral line less than width of light areas 9

9(10) 5–10 dark median parr marks along mid-dorsal line ahead of dorsal fin; few or no spots on tail; no red or yellow hyoid marks (in the two parallel grooves under the chin); black border of adipose fin with one or no breaks; hind margin of maxilla not reaching hind margin of eye .... Rainbow trout, *Salmo gairdneri* (p. 159)

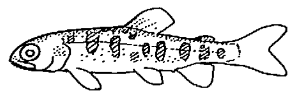


10(9) 4 or fewer (rarely 5) dark median parr marks (often none) ahead of dorsal fin; usually some black spots on caudal fin, particularly at base; red or yellow hyoid marks in the two parallel grooves under the chin (often absent in very young and in preserved fish); black border of adipose fin usually with one or more breaks; hind margin of maxilla may reach to or past hind margin of eye (not in very small fish) .... Cutthroat trout, *Salmo clarki*

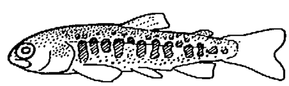


11(2) Dorsal fin without dark spots, and first dorsal ray not black (lake trout over 3 inches long may have faint dark bars on the dorsal) .. 12

12(13) Parr marks along lateral line are vertical bars, width of dark areas usually equal to, or less than width of light areas; predorsal distance about equal to one-half the standard length .... Lake trout, *Salvelinus namaycush* (p. 137)

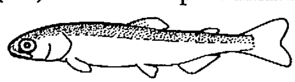


13(12) Parr marks along lateral line are irregular blotches, width of dark areas along lateral line greater than width of light areas; predorsal distance less than one-half the standard length .... Dolly Varden and Arctic char, ... *Salvelinus malma* and *Salvelinus alpinus* .... (p. 149 and p. 143)



14(1) Major rays in anal fin 13–19 (rarely 12) 5

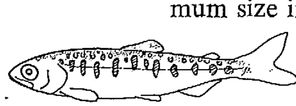
15(16) No parr marks; maximum size in fresh water about 2 inches .... Pink salmon, *Oncorhynchus gorbuscha* (p. 183)



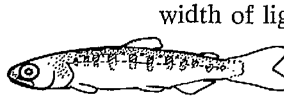
16(15) Parr marks present 17

17(20) Parr marks small, oval-shaped, none much higher than vertical eye diameter 18

18(19) No greenish iridescence on sides below lateral line; width of dark areas along lateral line about half width of light areas; some of the parr marks divided into roughly equal halves by lateral line; maximum size in fresh water about 18 inches in landlocked races, and about 8 inches in anadromous forms .... Sockeye salmon, *Oncorhynchus nerka* (p. 165)

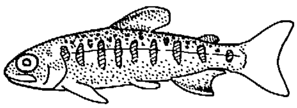


19(18) Mottled green on back, sides silver with faint green iridescence below lateral line; width of dark areas along lateral line more than half width of light areas; parr marks faint or absent below lateral line; maximum size in fresh water about 2½ inches .... Chum salmon, *Oncorhynchus keta* (p. 179)

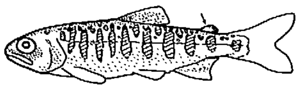


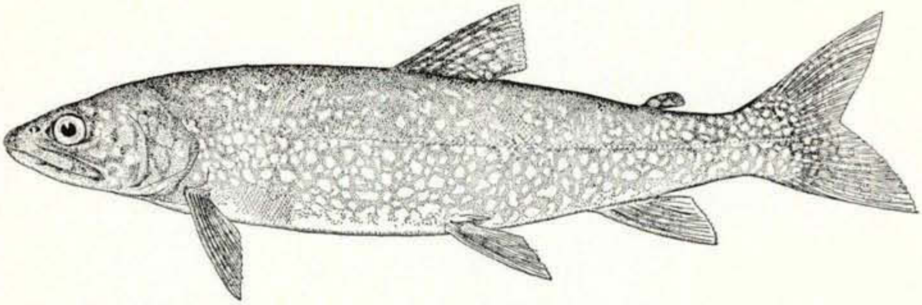
20(17) Parr marks tall bars, the highest much higher than vertical eye diameter 21

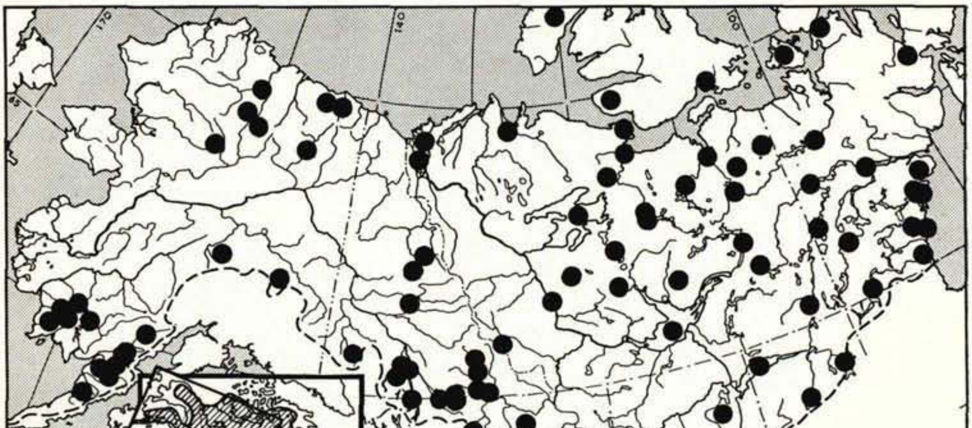
21(22) Adipose fin uniformly pigmented; anal fin usually with some dark pigment behind the white leading edge; usually 45–80 pyloric caeca .. Coho salmon, *Oncorhynchus kisutch* (p. 171)



22(21) Adipose fin with a clear unpigmented "window"; anal fin usually without dark pigment behind the white leading edge; usually 135–185 pyloric caeca ....
Chinook salmon, *Oncorhynchus tshawytscha* (p. 175)






SALVELINUS
NAMAYCUSH
MILES
400
KILOMETRES
600

LAKE TROUT

Salvelinus namaycush (Walbaum)

Salvelinus is an old name for char and *namaycush* is an Indian name. The French common name for this species is *touladi.*

Distinguishing Characters

The irregular whitish spots (never pink) on the back and sides, the deeply forked caudal fin, and the large number of pyloric caeca (93–198).

Description

Body typically troutlike, the depth usually less than the head length; head moderate, usually a little more than one-quarter standard length; snout rounded in young fish but becoming longer and pointed in large fish, snout 3.5–4.7 into head length; eye moderate (about 4 into head) in small fish, but proportionately much smaller in large fish (5–7 into head). Mouth large, slightly oblique, maxillary extends well past posterior margin of eye; well-developed teeth in both jaws, on head of vomer, on palatines, and tongue; numerous teeth on basibranchial bones. Branchiostegals 11–14 + 10–13; gill rakers moderate 5–9 + 11–15. Dorsal fin with 8–10 major rays; 8–10 major anal rays; 14–17 pectoral rays; and 9–11 pelvic rays. Dorsal fin farther back than in other chars, its origin closer to the caudal flexure than to the tip of the snout. Caudal fin deeply forked, the shortest ray less than half the longest. Scales small, cycloid, 116–138 pores in lateral line. Vertebrae 61–67. Pyloric caeca 93–198.

Size: Length to at least 122 cm (48 inches) and weight to 46.4 kg (102 lb) (a fish netted in Lake Athabasca) but usually much smaller.

Sexual dimorphism: No obvious external differences between sexes. Vladykov (1954) has reported "pearl organs" near the base of the anal fin in lake trout (both sexes) during the breeding season.

Colour: Variable in adults depending, at least in part, on size and habitat. The back is dark green to grey, or brown, and gradually shades into pale underparts that may be dirty white to a pale yellow. Dorsal surface and sides with irregularly shaped pale spots. Paired fins dusky with a pale leading edge. Dorsal and caudal fins dusky, often with distinct bars of darker pigment.

Young fish with 5–12 dark parr marks and immaculate fins (dark bars appear on the dorsal fin of young at about 3 inches in length). In small fish the parr marks are irregular dark blotches rather than distinct bars, and the pale spots on the back often form vermiculations. The width of the dark areas along the lateral line are usually equal to or less than the width of the pale areas.

Distribution

Found only in North America, and almost entirely within the limits of Pleistocene glaciation. South of the St. Lawrence River, Great Lakes, and Hudson Bay drainages they occur in Nova Scotia, New Brunswick, some headwater lakes of Atlantic drainages as far south as the Hudson River, in some Wisconsin and Minnesota lakes a few miles south of the Mississippi – Great Lakes divide, and in the extreme northwestern headwaters of the Missouri River in Montana. In the upper Fraser River, and other Pacific drainages from Skeena River northwest to Susitna River. In Bristol Bay drainages; in the upper but not the lower Yukon River basin. In northern Alaska, along the Brooks Range but not in coastal lowlands. Along the Canadian arctic coast they extend out onto several islands of the Archipelago, and range eastward to Labrador. Widely introduced outside its natural range. Detailed locality records given in Lindsey (1964).

Taxonomic Notes

The generic name of the lake trout is still a matter of controversy. For many years the lake trout was placed in a separate genus, *Cristivomer*, but most ichthyologists now place it in the genus *Salvelinus* to emphasize its close relationship to other chars. However, some experts (Vladykov, 1963) still retain *Cristivomer* as a distinct genus. The details of this argument are presented in papers by Morton and Miller (1954) and Vladykov (1963). The differences between the lake trout and other

Lake trout. Photo: L. Johnso

chars are largely matters of degree, and although in this marginal case a reasonable argument can be made for maintaining a separate genus for the lake trout, we choose to place it with the other chars in the genus *Salvelinus*. Amongst North American chars, the lake trout is the closest relative to the Eurasian genus *Hucho* (Lindsey, 1964).

The lake trout was originally named from Hudson Bay by Walbaum in 1792 as *Salmo namaycush*. Synonyms include *Cristivomer siscowet* and a number of other names that have not been used in many years. In the Great Lakes region three subspecies, *namaycush*, *siscowet*, and *huronicus*, are sometimes recognized (Hubbs and Lagler, 1964). The latter two are deepwater forms.

Whether there is morphological variation over the range of the lake trout consonant with its derivation from more than one glacial refuge has yet to be determined.

Postglacial Dispersal

The lake trout probably attained its present distribution by postglacial dispersal from both a northern Bering and a southern Mississippi refuge. An eastern refuge may also have existed on the Atlantic coast. Lindsey (1964) has discussed possible reasons why lake trout have failed to reach and cross Bering Strait; these include the absence of suitable ecological conditions (particularly for spawning) in lowland areas, and susceptibility of lake trout to attack by large sea-run lampreys (as evidenced by the drastic decline of lake trout in the Great Lakes after entry of the Atlantic sea lamprey).

Biology

The lake trout is usually considered an inhabitant of deep cold lakes. This is true in southern areas, but in our area, and probably over much of its range, the lake trout is not restricted to deep lakes. It is abundant in shallow tundra lakes and large clear rivers. It has, however, been taken on the bottom in 467 m (1400 ft) of water in Great Bear Lake, where it was feeding on the relict shrimp *Mysis* (L. Johnson, personal communication).

The food of adult lake trout consists of other fishes, bottom organisms, plankton, and terrestrial insects. They are often found gorged with small ciscoes, round whitefish, and sticklebacks (*Pungitius*). There are many small lakes on the Barren Grounds in which only lake trout occur. In such lakes it is not uncommon to catch lake trout that have made a meal of other lake trout only a few inches smaller than themselves. Little is known about the feeding habits of small lake trout, but they appear to eat mainly crustaceans, particularly *Mysis relicta* where it is present.

Growth rate of lake trout in our area is slow relative to more southerly areas. The data of Kennedy (1954) indicate that in Great Slave Lake trout of 5 lb are probably over 9 years old, and that it takes at least 17 years for a trout to reach 20 lb. In Great Bear Lake the growth rate is much slower.

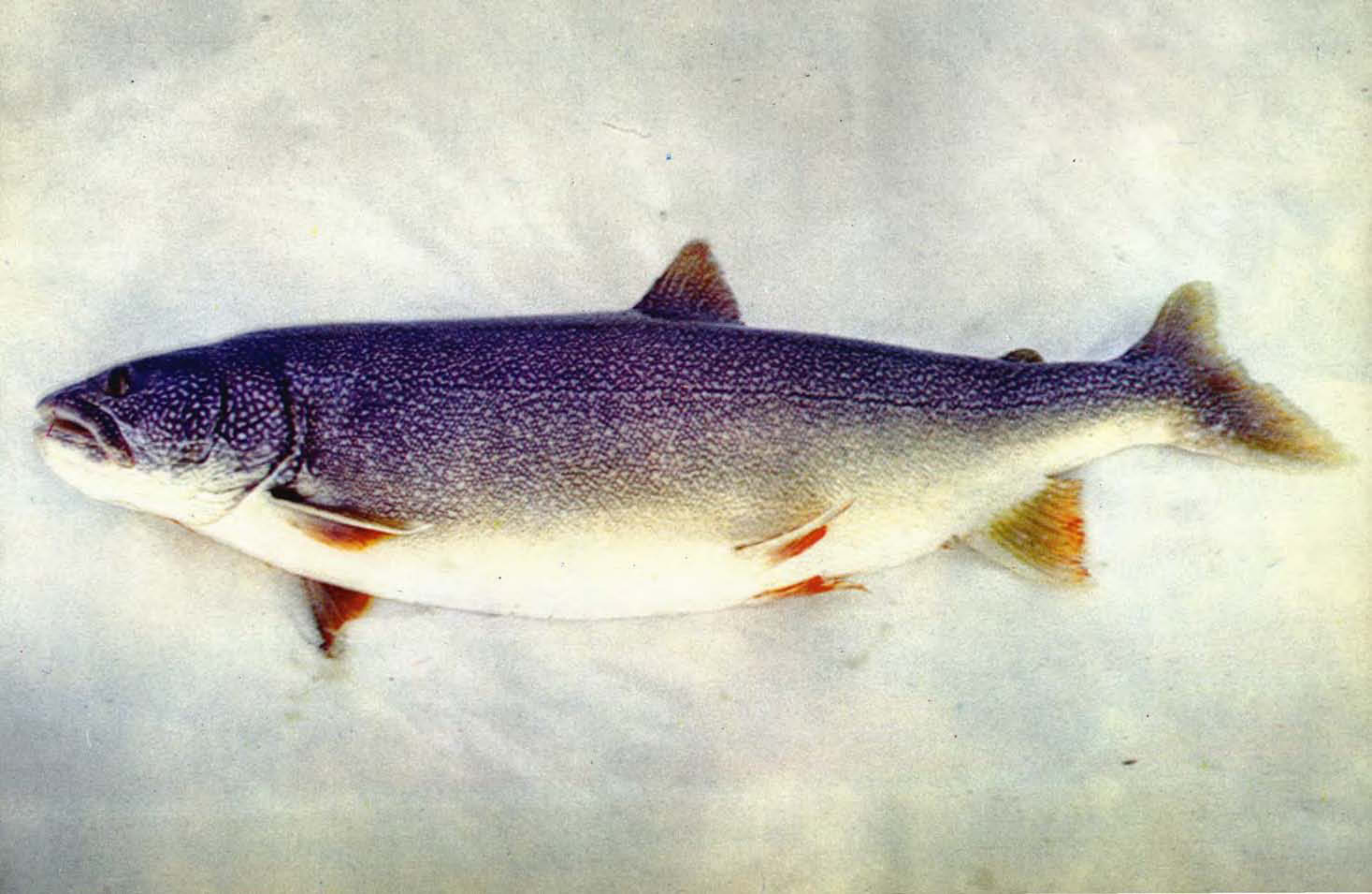
In Great Slave Lake some lake trout are mature at about 5 years and most are mature by their 11th year. The maximum age recorded in our area is 25 years, but older specimens probably exist. Spawning occurs in late summer and early autumn. No one has described the spawning of lake trout in the north. Most spawning probably occurs in lakes, although river spawning populations are known from Lake Superior and in southern Quebec north of Hull (D. E. McAllister, personal communication) and may also exist in our area.

Royce (1951) has described the spawning behaviour of lake trout in New York. There lake trout congregate over rubble or gravel areas along the lake shore. Suitable areas are often associated with windy points. The males arrive on the spawning grounds earlier than the females, and often clear loose sand and mud from the spawning area. No redd is built and eggs are simply extruded over the bottom. Usually more than one male is associated with a spawning female. The males approach the female, press against her sides, and begin quivering. At this time the dorsal fins of the males are held erect. The fertilized eggs become lodged in crevices in the rubble on the bottom.

Adult lake trout apparently continue to feed during the spawning season. A large female may contain up to 17,000 eggs, and probably spawns these in several different lots during a single spawning season. The eggs are quite large (4–5 mm in diameter) and in New York take about 4 months to develop. Mature females do not spawn every year; in Great Slave Lake most females appear to spawn every 2nd year, and in Great Bear Lake they may spawn every 3rd year. In lakes the young lake trout remain in shallow water along the shores for several years before moving into deeper water.

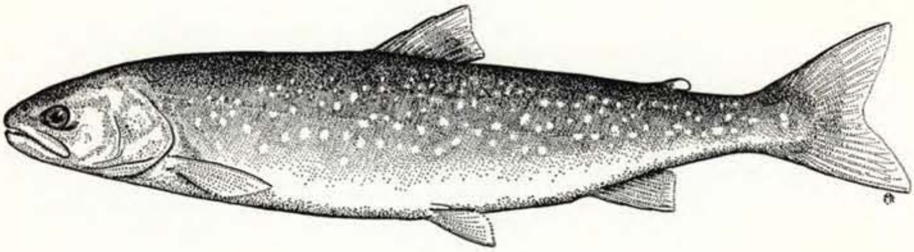
The flesh of lake trout is excellent, and may be canned. Lake trout support substantial commercial fisheries in Great Slave Lake and in an increasing number of lakes in the Northwest Territories, both in summer and winter; fresh lake trout from some lakes command high enough prices to cover costs of air transport to Hay River, from where they are trucked to southern markets. Lake trout are second only to whitefish in commercial value amongst freshwater species in our area.

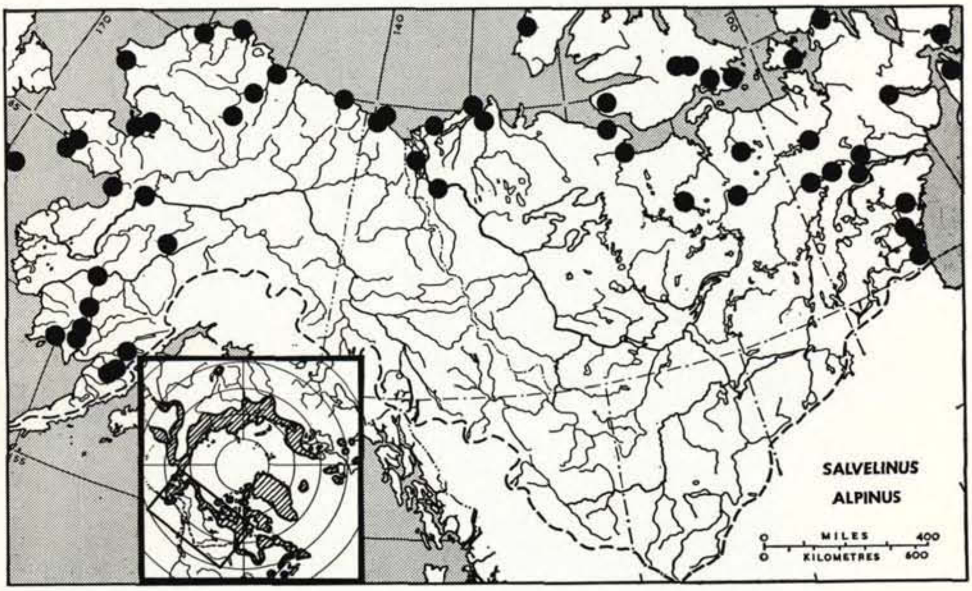
Sport fishing for lake trout is a growing tourist attraction. Because lake trout come into relatively shallow water during summer in the north, the deepwater trolling equipment used in the south is unnecessary. Preble (1908) wrote "Athabaska Lake, the Eastern and Northern arms of Great Slave Lake, and Great Bear Lake abound especially in these fine trout, and as the water is there beautifully clear the traveler frequently sees them pursuing their prey in the depths, or lying motionless



near the bottom. In the swift streams which enter these lakes, and in some which fall into the Arctic Sea, the pools at the foot of rapids are always tenanted by these voracious fish." Resorts serviced by float-equipped aircraft now operate in the Northwest Territories. To sustain the yield of lake trout, catches must be regulated, as the very slow growth and late maturity of these fish in northern waters render them liable to damage by excessive sport or commercial fishing.

Lake "trout" is of course a misnomer, as the fish is a char (*Salvelinus*), not a trout (*Salmo*). It is also known as lake char, grey trout, or in eastern Canada, as togue. The French common name comes from Lake Touladi in Temiscouata County, Quebec (Legendre et al., 1964).




SALVELINUS
ALPINUS
MILES 400
KILOMETRES 600

ARCTIC CHAR

Salvelinus alpinus (Linnaeus)

Alpinus means *of the mountains.* The French common name for this species is *omble chevalier.*

Distinguishing Characters

The large round spots (usually a violet–pink colour) usually greater in diameter than pupil of the eye, on the back and sides, and high number of gill rakers (12–19 on the lower limb of the first gill arch).

Description

Body typically troutlike, the depth usually less than the head length; head moderate, about one-quarter standard length or less; snout rounded, moderate, horizontal orbit diameter about equal to snout length. Mouth moderate to large, slightly oblique, maxillary usually reaching past posterior margin of eye, but in some nonmigratory populations maxillary does not reach posterior margin of eye; lower jaw develops a distinct hook in the breeding males of some populations; well-developed teeth in both jaws, on head of vomer (Fig. 18B), on palatines (space between vomerine and palatine teeth variable), and on tongue; teeth on basibranchial bones extremely variable, 20–85. Branchiostegals 10–12 + 10–13; gill rakers moderate 7–11 + 12–19. Dorsal fin with 10–12 major rays; 8–11 major anal rays; 14–16 pectoral rays; and 9–11 pelvic rays. Scales small, cycloid, 123–152 pores in lateral line. Vertebrae 60–71. Pyloric caeca 20–74.

Size: Length to 96 cm (38 inches) and weight to 11.8 kg (26 lb), but usually much smaller. Larger char have been reported from the USSR (Berg, 1948–49) and probably also occur in our area. In some nonmigratory populations mature adults are less than 200 mm (8 inches) long.

Sexual dimorphism: No obvious differences between sexes except at spawning time. Spawning males in some anadromous populations develop a hooked lower jaw (kype).

Colour: Colour is extremely variable and depends (in part) on size and habitat. In fresh sea-run adults the back is dark blue and the sides and underparts are silvery. In nonmigratory specimens the back is dark blue to olive green or brown and the sides and underparts are white, dusky, or, in breeding fish (and permanently in some populations on the Kenai Peninsula, Alaska) the sides are bright red. Dorsal surface and sides usually with violet–pink or red spots (the spots are less numerous and those along the lateral line are larger than in *S. malma*); some individuals completely lack spots and in some populations the spots are surrounded by a distinct halo with a bluish hue. Usually many spots are greater in diameter than the pupil of the eye. Paired fins usually immaculate, but in breeding fish and occasionally permanently, with creamy white leading edges followed by one band of dark and one of red pigment. Dorsal and caudal fins dusky; anal fin usually immaculate, but in breeding fish and also occasionally permanently, with a creamy white leading edge followed by a dark stripe and then red pigment.

Young and dwarf adults with 8–15 irregular wide dark parr marks, the combined width of the dark areas along the lateral line greater than the light. In very small fish (up to 3 inches long) the parr marks are irregular dark blotches rather than distinct bars. Fine dark speckling along the lower side. Dorsal fin clear, adipose only dusky.

Distribution

Circumpolar, including Iceland, the British Isles, Europe, northern USSR, south to Kamchatka. In North America from Kenai Peninsula and Kodiak Island, Alaska, around the Bering and arctic coasts to Newfoundland, the Gulf of St. Lawrence, and Greenland. There are isolated, relict populations in Quebec, New Brunswick, Maine, and New Hampshire. Abundant in coastal regions within our area, and on islands of the Canadian Arctic Archipelago.

Taxonomic Notes

The Arctic char was originally named from northern Europe by Linnaeus in 1758 as *Salmo alpinus*. Most workers now place it in the genus *Salvelinus* although a few Scandinavian ichthyologists still retain it in the genus *Salmo*. Synonyms include *S. rossii, S. stagnalis, S. naresi, S. arcturus, S. aureolus, S. oquassa,* and *S. marstoni*. The last three forms are recognized as valid species by many workers (Vladykov, 1963; Rounsefell, 1962), but they cannot be distinguished morphologically from *S. alpinus,* and are probably best treated as relict populations of the Arctic char.

Arctic char are plastic morphologically and many distinctive populations occur throughout the range of this species. Until more information is available subspecific names should be avoided. In our area, the Arctic char of the Bristol Bay region of Alaska are characterized by high gill-raker (population means of 15–17) and pyloric caeca (population means of 36–53) counts. From the Kuskokwim River north to the

Arctic char.
Photo: S. D. MacDonald, National Museums of Canada.

Mackenzie Delta region the Arctic char have characteristically low gill-raker (population means of 13–14) and pyloric caeca (population means of 27–31) counts. East of the Mackenzie system high gill-raker and pyloric caeca counts reappear, and remain relatively constant over the rest of the North American range of *S. alpinus*. These differences probably reflect periods of isolation caused by the Pleistocene glaciation (see following section). The relationship of the Arctic char to the Dolly Varden (*S. malma*) is discussed under the "Taxonomic Notes" section on the latter.

Postglacial Dispersal

McPhail (1961) interpreted morphological variation in North American populations of Arctic char in terms of geographic isolation in several glacial refuges. The western form of Arctic char is found in the Bristol Bay region and unglaciated portions of Kodiak Island and the Kenai Peninsula. Apparently this form of *S. alpinus* survived glaciation in these areas and has not greatly expanded its range postglacially. The form characterized by low gill-raker and pyloric caeca counts probably survived glaciation in the lower Yukon area and the unglaciated portions of northern Alaska. This form has postglacially expanded its range eastward and has met and probably introgressed with (along the arctic coast east of Mackenzie delta) a high count form that survived glaciation in the unglaciated northern Atlantic coastal area. This eastern form of Arctic char had dispersed postglacially north and west along the arctic coast, but left relict populations in Quebec, Maine, New Hampshire, and the Maritime Provinces.

Biology

In our area Arctic char occur both as anadromous and landlocked populations. The anadromous populations spend considerable time in the sea, but apparently do not migrate far from the mouths of rivers. The landlocked forms occur mainly in lakes. At some times of the year Arctic char are abundant in the estuaries and rivers along the entire arctic coast, but apparently seldom penetrate more than 50 miles inland. In the Bristol Bay region Arctic char appear to be confined to lakes. In the Kuskokwim and Yukon systems scattered populations are found in lakes and clear rivers. North of the Yukon system anadromous populations are abundant.

Arctic char are carnivorous. The adults feed mainly on small fishes and bottom organisms (particularly gastropods and chironomid larvae). Young char feed more heavily on amphipods and insect larvae (Nilsson, 1965). The growth rate of Arctic char is slow, and varies from area to area. Landlocked populations grow much more slowly than anadromous populations. In the eastern arctic it takes from 10 to 15 years for anadromous Arctic char to reach 5 lb in weight. No information is available on growth rate in the western Arctic, but it is probably faster. Sprules (1952) reports

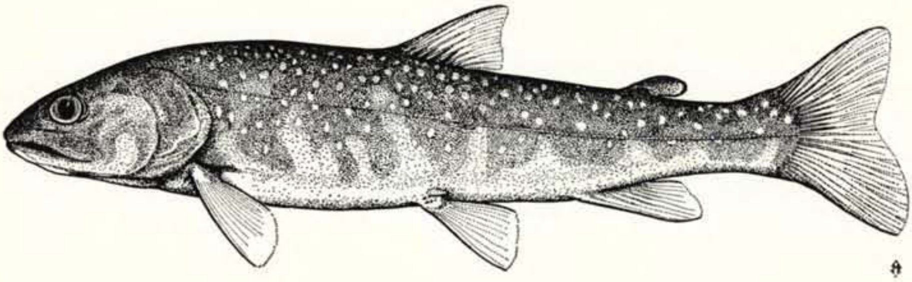
15-year-old landlocked char from near Term Point, on Hudson Bay, that weighed only 624 g (22 oz).

Grainger (1953) indicates that the anadromous Arctic char of Frobisher Bay, Baffin Island, mature in their 12th year, but those from George River, Ungava Bay, mature earlier (their 7th year or younger). The landlocked population studied by Sprules (1952) matured in their 2nd or 3rd year. The oldest char recorded from the North American arctic were at least 24 years old. Spawning occurs in the autumn. The migration of anadromous populations starts in late July and continues into September. Spawning takes place over gravel beds in lakes and in pools below rapids in rivers. The spawning behaviour of the North American Arctic char has not been recorded, but Fabricius (1953) and Fabricius and Gustafson (1954) have studied spawning behaviour in Scandinavian populations of *S. alpinus*. Males establish and guard territories. The female chooses the spawning site (usually walnut-sized gravel), and digs a redd (nest) by turning on her side and beating violently with her tail. The male courts the female by circling her incessantly and brushing lightly against her sides. When the female is ready to spawn she lowers her anal fin into the nest, and then the male and female swim side by side across the nest, quivering and extruding eggs and milt. After one to five spawnings the female undulates over the nest, forcing the eggs down into crevices between the gravel. She then covers the nest, usually by digging another nest nearby. Spawning occurs during daylight hours, and one male usually spawns with more than one female. The male char remain near the nests after spawning; Sprules (1952) describes the Eskimo method of spearing them through the ice.

The eggs are quite large (3–4 mm in diameter) and a large female may contain as many as 7200. Mature females normally do not spawn every year. The eggs apparently incubate over winter, as Sprules indicates that eggs spawned in autumn can still be seen the next spring just before ice breakup. The seaward migration of adults that spawned the previous autumn occurs in late spring at about the time of breakup. The young char remain among the rocks along the shores of lakes and streams for several years. The first migration seaward occurs from the 5th to 7th year.

Arctic char are used extensively by coastal Eskimos for human and dog food. The Eskimos fish for them with handlines, jigs, spears, gillnets, and traps. Winter-caught fish are frozen for later use, and the summer catch is either used fresh or occasionally smoked or salted. The Eskimos eat the entire fish, including the head, which is considered a delicacy. At present there are a number of Eskimo cooperatives in the eastern arctic that fish char commercially. Most of the catch is frozen and shipped south to large population centres where it is sold as a delicacy; some is canned. In addition to the commercial fishery there is a growing sport fishery for Arctic char. The species strikes readily at artificial lures and puts up a good fight. Two of the most important sport fisheries are at Cape Dorset and Tree River. Sport and commercial fishing must be carefully controlled because of the very slow growth of the Arctic char.

The word char is generally spelled in England as "charr." D. E. McAllister (personal communication) suggests that in deference to the pronunciation of those anglers who habitually pursue it in Scotland, the word should be spelled as "charrr."




SALVELINUS
MALMA
MILES
0 400
KILOMETRES
0 600

DOLLY VARDEN

Salvelinus malma (Walbaum)

Malma is a vernacular name in Kamchatka. The French common name for this species is the same as the English.

Distinguishing Characters

The small round spots (yellow, orange, or pink, and usually smaller than pupil diameter) on the back and sides, and the low number of gill rakers (8–14) on the lower limb of the first gill arch.

Description

Body typically troutlike, the depth less than the head length; head moderate, about one-quarter standard length; snout rounded, moderate in small fish (about equal to horizontal orbit diameter) but disproportionately longer and more pointed in larger fish. Mouth large, slightly oblique, maxillary usually reaching past posterior margin of eye, but not in some nonmigratory populations; lower jaw develops a distinct hook in the breeding males of some populations; well-developed teeth in both jaws, on head of vomer, on palatines (space between vomerine and palatine teeth variable), and on tongue; teeth on basibranchial bones variable, 0–44. Branchiostegals 11–15 + 10–15; gill rakers moderate, 3–10 + 8–14. Dorsal fin with 10–12 major rays; 9–11 major anal rays; 14–16 pectoral rays; and 9–11 pelvic rays. Scales small, cycloid, 105–142 pores in lateral line. Vertebrae 57–70. Pyloric caeca 13–47.

Size: Length to 127 cm (50 inches) and weight to 14.4 kg (32 lb), but usually much smaller (in our area most of the landlocked populations are dwarfed).

Sexual dimorphism: No obvious differences between sexes except at spawning time. Spawning males in some anadromous populations have a hooked lower jaw (kype).

Colour: Extremely variable and depends in part on size and habitat. In fresh sea-run adults the back is dark blue and the sides and underparts silvery. In nonmigratory specimens the back is dark blue to olive-green and the sides and underparts are white or dusky, but in breeding fish and permanently in some populations (e.g., Summit Lake on Kenai Peninsula, Alaska) the sides are bright red. Dorsal surface and sides with yellow, orange, or red spots (the spots are more numerous and those along the lateral line are smaller than in *S. alpinus*), and occasionally with vermiculations. Usually all spots are smaller in diameter than the pupil of the eye. Paired fins usually immaculate, but in breeding fish and occasionally permanently with creamy leading edges followed by one band of dark and one of red pigment. Dorsal and caudal fins dusky, occasionally with pale spots. Anal fin usually immaculate, but in breeding fish and also occasionally permanently with a creamy leading edge followed by a dark stripe and red pigment.

Young and dwarf adults with 8–12 rather irregular dark parr marks, the width of the dark areas along the lateral line greater than width of the light. In very small fish (up to 3 inches long) the parr marks are irregular dark blotches rather than distinct bars. Fine dark speckling along the lower sides. Dorsal and adipose fins may be dusky but lack distinct markings.

Distribution

Western North America and northeast Asia (from the Yalu River, Korea, north to the Anadyr River). On the Pacific slope of North America from the Sacramento system (McCloud River) and isolated streams in Nevada north to the Seward Peninsula; on the east slope of the Continental Divide from the upper Mackenzie system south to headwaters of the South Saskatchewan River. On Vancouver, Queen Charlotte, Kodiak, and many of the Aleutian islands. In our area anadromous and nonmigratory populations of Dolly Varden are found in the Bristol Bay region of Alaska, and isolated nonmigratory populations are found in mountainous areas in the headwaters of the Yukon and Tanana rivers, on the Seward Peninsula, and in headwaters of the Liard (including Nahanni River), Peace, and Athabasca rivers. There are numerous unverified reports of Dolly Varden in the headwaters of the Peel River and other Mackenzie tributaries that rise in the Richardson and northern Mackenzie mountains. None of these reports has been authenticated and it is not known whether the chars in this area are Dolly Varden or Arctic char. There are literature records of Dolly Varden from along the arctic coast of Alaska, but in the few instances when specimens were saved they have invariably proved to be Arctic char.

Taxonomic Notes

The Dolly Varden was originally named from Kamchatka by Walbaum in 1792 as *Salmo malma.* Since then it has been placed in the genus *Salvelinus.* Synonyms include the names *spectabilis, pluvius, tudes, parkei,* and a number of other names that have not been used in many years.

There has been debate as to whether the Dolly Varden represents a species distinct from the Arctic char (*S. alpinus*). They are very closely related, and many authors consider the Dolly Varden a subspecies of Arctic char and refer to it as *Salvelinus alpinus malma.* It is true that no characteristic is known that will separate all populations of Dolly Varden from all populations of Arctic char. However, in Alaska where their ranges overlap there are many lakes in which the species occur together, and under such conditions it is not difficult to distinguish the two. There is no evidence that they hybridize in nature. For this reason the Dolly Varden should be treated as a distinct species.

There are at least two morphologically distinguishable forms of Dolly Varden in our area (McPhail, 1961). In the Bristol Bay region and Seward Peninsula of Alaska, Dolly Varden have 65–71 vertebrae and 11–14 gill rakers on the lower limb of the first gill arch. The Dolly Varden of the upper Yukon system, and the Liard, Peace, and Athabasca rivers have 57–67 vertebrae and 8–12 gill rakers on the lower limb of the first gill arch. The differences between the two forms may be great enough to warrant subspecific recognition; however, until more information is available about the Asiatic forms of *S. malma,* it is probably best to avoid using subspecific names.

Postglacial Dispersal

The existence of two morphological forms of Dolly Varden in our area indicates postglacial dispersal from more than one refuge. McPhail (1961) suggests that the northern form of *S. malma* (now found in the Bristol Bay region and the Seward Peninsula) survived glaciation in the Bering refuge, and the southern form survived glaciation south of the ice sheet in the Pacific refuge. The southern form attained its present distribution in our area by postglacial dispersal northward from the Columbia system; its wide dispersal along the eastern slope of the Rocky Mountains suggests it may have crossed the Continental Divide from west to east at more than one place.

Biology

Little is known about the biology of Dolly Varden in our area. In the large lakes of the Bristol Bay region dwarf populations are common in tributary streams. However, larger, apparently anadromous specimens are often taken in estuaries in the same area. In the Yukon system scattered dwarf populations are found in clear streams and rivers. They are rarely taken in muddy water. The only population known from north of the Yukon system occurs in streams tributary to Salmon Lake on the Seward Peninsula. The Dolly Varden of the Athabasca and Peace systems are larger than those to the north, and are found in lakes, clear streams, and big muddy rivers.

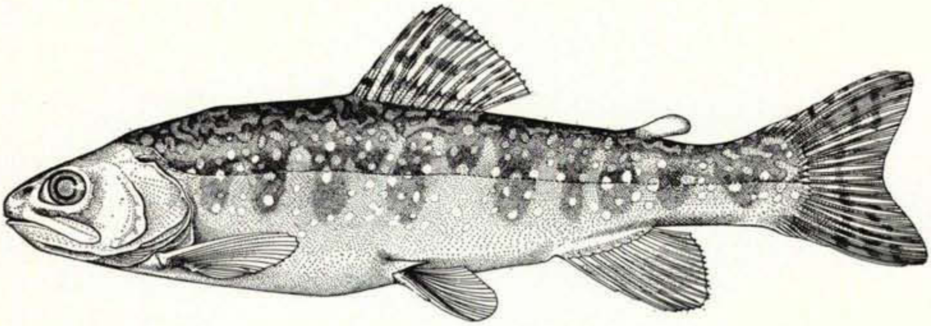
Adult Dolly Varden are carnivorous, and feed mainly on other fishes, aquatic insect larvae, and gastropods. In many lakes snails appear to be the main food of adult *S. malma.* Where Dolly Varden occur sympatrically with trout (*Salmo*) they feed mainly on bottom organisms and are rarely taken near the surface. The Dolly Varden has an undeserved reputation as a rapacious predator on young salmon (*Oncorhynchus*) and salmon eggs. In the past Alaska paid a bounty on Dolly Varden tails. However, in the few instances where the predation of Dolly Varden on young salmon has been studied carefully (e.g., Roos, 1959) it has been shown that they are not serious predators on young salmon. This does not mean that they do not eat young salmon and salmon eggs; they do, but not to the extent that they are likely to damage salmon stocks. Young Dolly Varden feed mainly on bottom organisms (small gastropods and insect larvae) but also on plankton. In the Athabasca system young Dolly Varden grow very rapidly, and reach a length of about 75 mm (3 inches) in their first 6 months and are almost 300 mm (1 ft) after 2 years (Bajkov, 1927). The growth rate in more northern landlocked populations is probably much slower, as the maximum size rarely exceeds 12 inches. In the Athabasca system sexual maturity is usually reached by the 3rd or 4th year.

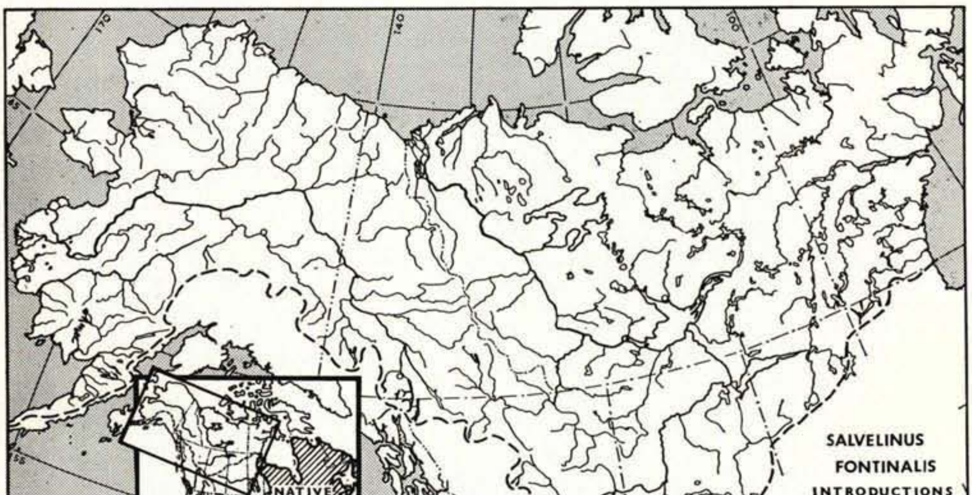
Spawning occurs in the autumn. Anadromous populations in southeastern Alaska begin to enter fresh water by June, but the run reaches a peak in September (Armstrong, 1965). In the Athabasca system the mature adults begin aggregating in streams in late August and September. Dolly Varden appear to be primarily stream spawners, but lake spawning populations may exist. The only published observations on the spawning behaviour of *S. malma* are those of Needham and Vaughn (1952). The spawning act appears to be similar to that described for *S. alpinus.* The female digs a redd in the gravel by turning on her side and beating with her tail. The male courts the female by swimming alongside her and quivering vigorously. During actual spawning both fish are side by side over the nest. They quiver, gape, and arch their backs as the eggs and milt are extruded. After one or more spawnings the female undulates over the nest, and then covers the eggs with gravel. As in the Arctic char, spawning occurs during daylight hours.

The eggs are quite large (about 5 mm in diameter), and a large female may contain up to 8000. They probably develop over winter and hatch in the early spring. The young fish usually remain in the shallow areas of streams and rivers for 2 or 3 years, and then move out into deeper water or into lakes. Most of the dwarf populations appear to spend their entire lives in rivers and streams.

The pink flesh of the Dolly Varden is excellent to eat. In areas where no trout occur Dolly Varden are considered good sport fish. They will strike readily at artificial lures and will occasionally rise for flies, but do not have the fighting quality of trout.

The name Dolly Varden derives from a young lady of that name in Charles Dickens' novel "Barnaby Rudge," who favoured bright dresses. A gay polka-dotted material named after her was in vogue in the American west, and settlers transferred the name to the fashionably attired *S. malma.* A less flattering alternative common name is "bull trout."




SALVELINUS
FONTINALIS
INTRODUCTIONS
NATIVE
MILES
KILOMETRES
0
400
0
600
170
140
100

BROOK TROUT

Salvelinus fontinalis (Mitchill)

Fontinalis means *living in springs*. The French common name for this species is *omble de fontaine*.

Distinguishing Characters

The red spots with blue halos, dark green marbling on back and dorsal fin, and deep body.

Description

Body deep, typically troutlike, its depth in adults equal to or greater than the length of the head; head moderate, slightly greater than one-quarter standard length; snout rounded, moderate in small fish, but disproportionately longer and more pointed in larger fish. Mouth large, slightly oblique, maxilla usually reaching well past posterior margin of eye. Well-developed teeth in both jaws, on head of vomer, on palatines, and tongue; usually no teeth on basibranchial bones. Branchiostegals 10–13 + 9–12; gill rakers moderate, 4–7 +10–15. Dorsal fin with 10–14 major rays; 9–12 major anal rays; 11–14 pectoral rays; and 8–10 pelvic rays. Caudal fin only slightly forked. Scales small, cycloid, 110–132 pored scales in lateral line. Vertebrae 58–62. Pyloric caeca 23–55.

Size: Length up to 86 cm (34 inches) and weight up to 6.6 kg (14.5 lb) but usually much smaller.

Sexual dimorphism: Mature males have longer pectoral and pelvic fins, and longer maxillae, than have females. Spawning males develop a hooked lower jaw (kype) and deeper body.

Colour: Colour is extremely variable. In fresh sea-run adults the back is dark green, the sides silvery, and the underparts white; the red spots are barely discernible on the sides. In nonmigratory populations the dark green marbling (vermiculations) are well developed on the back, on the dorsal fin, and often on the caudal. The sides bear a few red spots encircled in blue halos. The lower fins are dusky with a white stripe along the leading edges of the fins followed by a dark stripe. In breeding fish (particularly males) the sides are red and the lower fins are red with a distinct white leading edge followed by black. Often the mouth and lower surfaces of the body become dusky in breeding males.

The young have 8–12 wide dark parr marks along the sides (the widest about equal to the eye diameter) and often a few small red or yellow and sometimes blue spots. There are no prominent dark spots (other than the parr marks) below the lateral line. Some black on dorsal fin. Pelvic and anal fins with milky leading edge followed by dark streak.

Distribution

Native to North America, but widely introduced in temperate areas around the world. In North America originally from Hudson Bay (north to Seal River on the west side and Povungnituk on the east side) and Labrador, on Newfoundland, and south to Cape Cod on the Atlantic coast and inland to the Great Lakes. A few apparently natural populations in the upper Mississippi system south to northeastern Iowa, and south along the Appalachian Mountains to the headwaters of the Savannah, Chattahoochee, and Tennessee rivers in the Carolinas and Georgia. In our area introduced into the Athabasca and McLeod rivers (upper Mackenzie system). The natural northern limit on the west coast of Hudson Bay is close to the southern limit of our area, and occasional individuals may occur north of the Seal River.

Taxonomic Notes

The brook trout was originally named from New York as *Salmo fontinalis* by Mitchill in 1815. Since then it has been placed in the genus *Salvelinus,* and sometimes in the subgenus or genus *Baione.* Synonyms include the names *alleghaniensis, nigrescens, canadensis, hudsonicus,* and *timagamensis.* The aurora trout, *S. timagamensis,* of a restricted region in northern Ontario may represent a genetically distinct form; Sale (1967) believes it to be a subspecies.

Postglacial Dispersal

Brook trout evidently survived glaciation in southeastern North America, perhaps both in the Mississippi and on the Atlantic slope. They have entered our area only through the agency of man.

Biology

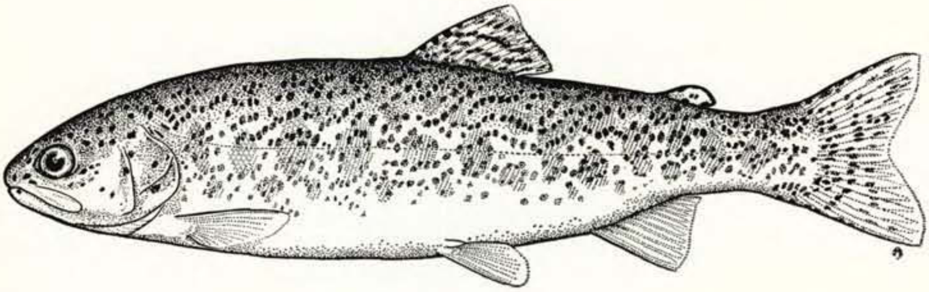
Little is known about the biology of the introduced brook trout in our area. Typically they are fish of cool, clear rivers, streams, and lakes; anadromous populations occur in rivers near the sea coast. They are most active in the early morning and late afternoon. During the day brook trout remain out of the current and lurk quietly behind rocks, or under overhanging logs and cutbanks. The adults feed mainly on terrestrial and aquatic insects but larger individuals also take small fishes. Anadromous adults in the sea feed mainly on amphipods and small fishes. Young brook trout feed on smaller organisms, particularly ostracods, copepods, and Cladocera. In southern areas brook trout grow fairly rapidly and reach about 75 mm (3 inches) in their 1st year; in Ungava they attain lengths of between 40 and 70 mm (Power, 1966). They usually reach sexual maturity in their 2nd year (males in their 1st year) and live up to 7 years.

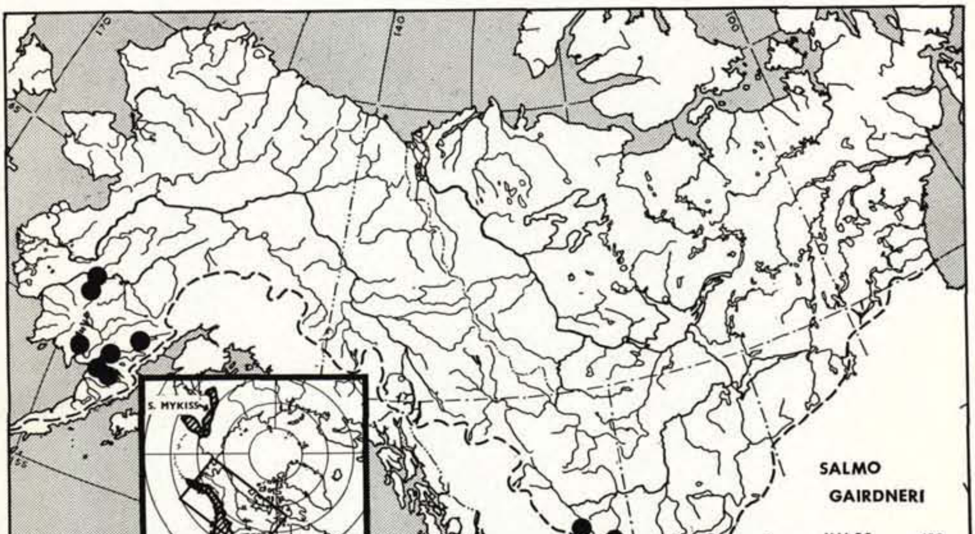
Spawning occurs in the autumn from late October to December in the south, but in early September in Ungava. Brook trout are primarily stream spawners, but like most trout and char they will spawn in lakes if there are gravel areas where ground water is upwelling. The usual spawning site is in a riffle over a gravel bottom. The female digs a redd in the gravel by turning on her side and beating with her tail. While the female is digging, a male takes up a position slightly downstream of the female and occasionally moves upstream alongside the female and quivers or nudges her and then glides back downstream. Both the male and female are aggressive at this time and drive away any intruders. However, the female appears to be aggressive only towards other females. When the female is ready to spawn she moves over the redd and lowers her anal fin down to the bottom. This apparently stimulates the male who darts to the side of the female and quivers vigorously. During actual spawning both fish are side by side over the nest. They quiver, gape, and arch their backs as the eggs and milt are extruded. Accessory males that have been kept off by the dominant male often rush in at this moment and also discharge milt. After spawning, the female undulates over the nest and covers the eggs with gravel. Both males and females may spawn several times, and with different mates, during a single spawning season.

The eggs of the brook trout are quite large (3.8–5 mm in diameter), and a large female may contain up to 5000. The eggs develop over winter, and hatching takes about 140 days at 36 F (2.2 C). After hatching, the alevins remain in the gravel until the yolk sac is absorbed. The fry usually emerge from the gravel in early spring. The young apparently remain in the general area of the nest until they reach a length of about 50 mm (2 inches).

The brook trout is one of the most highly prized freshwater game fish in eastern North America. It takes artificial lures readily, and once hooked is a strong fighter. Its rapid growth and maturity allow it to sustain heavy angling pressure in the south, but at its northern extremity it may be more susceptible to overexploitation.

This fish should correctly be called "brook char," but the name trout misapplied to this species (and also to another member of the genus *Salvelinus,* the "lake trout") is firmly established. Other commonly used names include "speckled trout" and "Eastern brook trout." In Newfoundland the nonanadromous form enjoys the names "mud trout" and "slob."

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S. MYKISS
SALMO
GAIRDNERI
MILES
400
KILOMETRES
600

RAINBOW TROUT; STEELHEAD TROUT (when anadromous)

Salmo gairdneri Richardson

Salmo is the Latin name for the salmon of the Atlantic and *gairdneri* is named after Dr Meredith Gairdner, a naturalist in the employ of the Hudson's Bay Company. The French common name for this species is *truite arc-en-ciel.*

Distinguishing Characters

The black spots on the back, dorsal fin, and caudal fin, and 12 or fewer rays in the anal fin. Any true trout (*Salmo*) caught in the area outlined in the introduction is probably this species.

Description

Body typically troutlike, somewhat compressed; head moderate, about one-quarter standard length or less; snout rounded (hooked in older males), slightly longer than horizontal eye diameter. Mouth large, slightly oblique; well-developed teeth in both jaws, on the head and shaft of vomer, on the palatines, and tongue; no teeth on basibranchials. Branchiostegals 10–13 + 9–12; gill rakers moderate, 6–9 + 11–13. Dorsal fin with 10–12 major rays; 8–12 major anal rays; 14–16 pectoral rays; and 9–10 pelvic rays (usually 10). Scales small, cycloid, 115–150 pored scales in lateral line. Vertebrae 61–66 (usually 63–65 in our area). Pyloric caeca 27–80.

Size: Sea-run specimens (steelhead) up to 122 cm (4 feet) in length and 16.3 kg (36 lb) in weight; nonmigratory fish (rainbows) usually much smaller, but known up to 23.6 kg (52 lb) (Jewel Lake, B.C.).

Sexual dimorphism: No striking external differences between sexes, but spawning males have a more vivid red lateral band than females, and often a more pointed or hooked snout.

Colour: Extremely variable and depends in part on size and habitat. In fresh sea-run specimens the back is dark blue and the sides and underparts silvery. In non-migratory specimens the back is bluish green to brown and the sides and underparts are white, dusky, or yellowish. There is usually a distinct lateral stripe that varies from light pink to vivid red. The dorsal, adipose, and caudal fins have bold dark spots, those on the caudal usually in radiating rows. The adipose is bordered either by a black continuous margin or by several black spots. Dorsal and pelvic fins often with white or orange leading edges. Usually no red hyoid streaks on underside of jaw, but in the Bristol Bay region this character is often well developed, and reddish irregular streaks occur on some trout from Summit Lake north of Prince George.

Young and dwarf adults (up to 10 inches) have 8–13 dark parr marks on the sides, the width of the dark areas along the lateral line less than the width of the light. There are also 5–10 dark oval parr marks on the midline between the dorsal fin and the head. No dark spots other than the parr marks below the lateral line. Dorsal fin with dark leading edge in small fry; a series of distinct dark bars or spots in older fish. Distinct white or orange tip to dorsal and anal fins. Few or no spots on tail.

Distribution

In North America on the Pacific and Bering slopes from northwestern Mexico to the Kuskokwim River, Alaska, and on the east slope of the Continental Divide in headwaters of the Peace and Athabasca rivers. Possibly also in Kamchatka and Okhotsk Sea drainages (as *"Salmo mykiss"*). Widely introduced in other parts of the world. In our area rainbow trout occur naturally in the Bristol Bay region, the southern tributaries of the Kuskokwim River (Aniak and Kisaralik rivers), and in the headwaters of the Peace and Athabasca rivers (Mackenzie system). They have been introduced with some success in a number of lakes in the upper Yukon near Whitehorse, Mayo, and Dawson City, and in the Fairbanks area (Tanana system).

Taxonomic Notes

The rainbow trout was originally named from the Columbia River at Fort Vancouver by Richardson in 1836 as *Salmo gairdneri.* The most commonly used synonym is *Salmo irideus.* In addition a host of names (including *gilberti, rosei, aquilarum, regalis, kamloops, stonei,* and *whitehousei*) have been used as either specific or subspecific names for trout of the rainbow type. Because of the confused taxonomy of the rainbow trout complex, it seems best at present to follow Needham and Gard (1959) and not use subspecific names, although some may well be shown to be valid. Behnke (1966) has indicated the close relationship between the North American trout and the trout of Kamchatka (*Salmo mykiss*), and suggested that they may be the same species. However, because of nomenclatorial difficulties (*S. mykiss* has priority, and the name was at one time erroneously used for cutthroat trout), Behnke suggests that at this time it is better not to synonymize *S. gairdneri* with *S. mykiss*.

Rainbow trout in the Kuskokwim River, and also in the upper Peace River, have some red pigment in the hyoid grooves beneath the lower jaw, a character that is typical of the cutthroat trout *S. clarki* whose range lies farther south. Rainbow trout in these two drainages may also differ in other morphological characters; larger samples are required for study.

The common name steelhead is useful to distinguish the anadromous from the nonmigratory forms of the rainbow trout. Nonmigratory rainbows receive many different common names (such as "Kamloops trout") from anglers, but distinctions between these various forms are usually clearer to the fishermen than they are to scientists.

Postglacial Dispersal

The present distribution of the rainbow trout suggests that it survived glaciation in two refuges: the Pacific coast south of glaciation, and the Bering area north of the Alaska Peninsula. The isolated populations in northern Mexico and the Colorado system are probably relicts of a formerly more widespread southern range that has contracted postglacially. In our area the rainbow trout probably survived glaciation in the Bristol Bay region and postglacially has not significantly expanded its range in this area. The rainbow trout of the Peace and Athabasca rivers are probably derived from populations that dispersed postglacially north from the Pacific refuge and subsequently crossed the Continental Divide into these rivers, perhaps at more than one point.

Biology

Virtually nothing is known about the biology of the rainbow trout in our area. Most of the populations appear to be nonmigratory, but anadromous populations (steelhead) may occur in the Bristol Bay region. In Alaska north of the Alaska Peninsula rainbow trout are most commonly found in clear rivers and streams, particularly near the outlets of lakes and below waterfalls or rapids. Adult rainbows feed mainly on aquatic insect larvae (particularly caddis and black flies), molluscs, crustaceans, and occasionally small fishes. In Alaska adult rainbow trout feed on salmon eggs and young salmon at certain times of the year. Young trout feed on similar but smaller organisms.

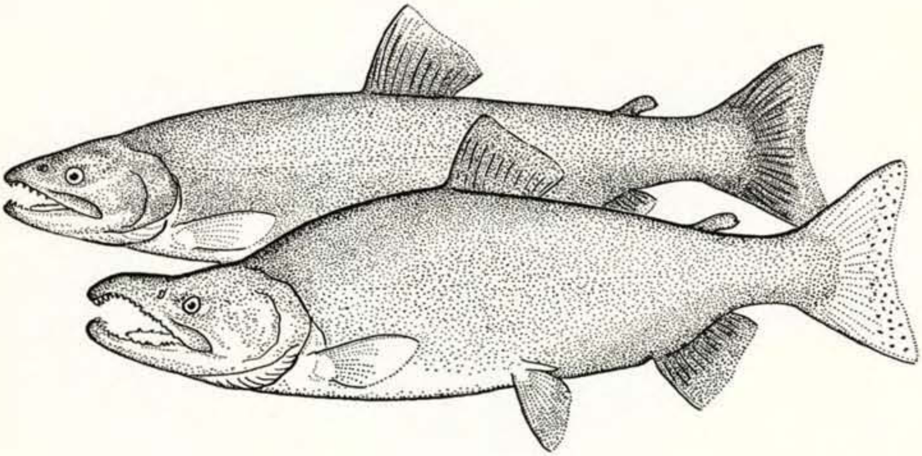
Little is known about the growth rate of rainbow trout in our area. In the Athabasca system rainbow trout reach a length of about 10 cm (4 inches) at the end of their 1st year, and take about 6 years to reach 30 cm (1 ft) in length. The fish in the Bristol Bay region may grow more rapidly, and reach a much larger size. In British Columbia, rainbow trout usually reach maturity in their 3rd or 4th year. The males often reach sexual maturity a year earlier than the females. Anadromous populations (steelhead) spend from 1 to 4 years in fresh water, and then migrate to the sea where they may spend from 1 to 4 years before returning to spawn.

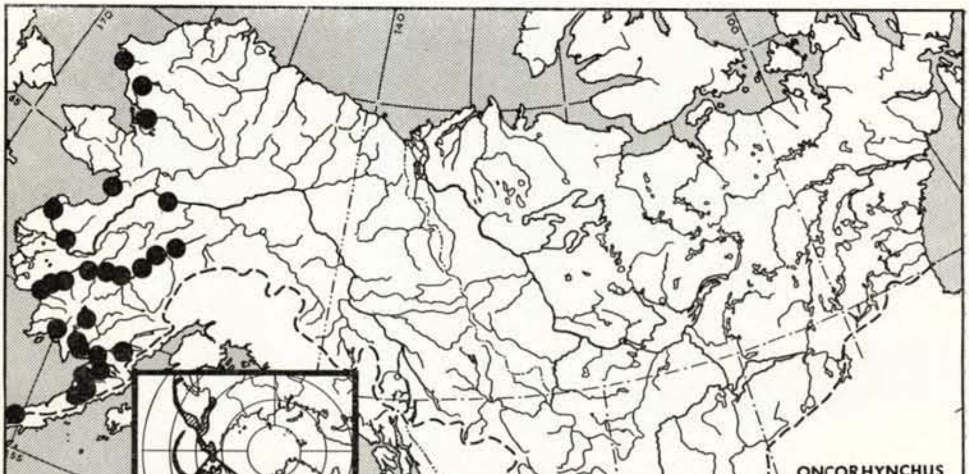
Spawning occurs in the early spring; the first fish start moving into the spawning streams before ice breakup. The female chooses the spawning site, and builds a redd by turning on her side and beating with her tail. The redd is usually built in a gravel area at the head of a riffle just below a pool; it is a roundish depression in the gravel, usually about 4–12 inches in depth and about 15 inches across. There are usually several males associated with each female, but normally one male is dominant and keeps others at a distance. The dominant male courts the female by moving alongside her and quivering. When the female is ready to spawn she drops into the redd and lowers her anal fin into the deepest part. The male moves beside her so that their vents are opposite. Both fish then arch their backs and gape as the eggs and milt are extruded. The female then covers the nest by digging gravel upstream that is washed down over the eggs. It takes several spawnings to empty the ovaries of the female.

The eggs are large (3–5 mm in diameter). Big anadromous (steelhead) females may contain as many as 7600; in nonmigratory populations the females usually lay fewer than 2000 eggs. The fertilized eggs develop in the gravel for about 2 months (depending on the water temperature), and the young emerge from the gravel during the summer (late June through September). In lake-dwelling populations most of the fry move into the lake during their first summer or autumn. However, some fry may spend the winter in the spawning streams and enter the lake as fingerlings the next spring. In stream-dwelling populations (which apparently most of the populations in our area are) the young move into riffle areas in the streams. They remain there during the summer but tend to move into pools during the autumn and winter. This seasonal shift in habitat is particularly notable in streams where rainbow trout and coho salmon occur together.

The rainbow trout is the most highly prized freshwater gamefish in western North America. It strikes vigorously at artificial lures and natural baits, and in some waters will rise readily to artificial flies. The rainbow trout's beauty, strength, endurance, and spectacular leaps have caused many anglers to consider it the finest of trouts.

The flesh of the rainbow varies from bright red to white, but regardless of colour it is usually excellent. There is no commercial fishery for rainbow trout in our area, but its qualities as a sports fish make it a very valuable species.

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ONCORHYNCHUS
NERKA
0 MILES 400
0 KILOMETRES 600

SOCKEYE SALMON; KOKANEE (when nonanadromous)

Oncorhynchus nerka (Walbaum)

Oncorhynchus means *hooked snout* and *nerka* is a Russian name. The French common names for this species are *saumon nerka* and *kokani.*

Distinguishing Characters

The absence of black spots on the back or caudal fin, and the 19–27 long, slender, serrated gill rakers on the lower limb of the first gill arch.

Description

Body typically troutlike, somewhat compressed; head moderate, about one-quarter standard length except in spawning males where the snout is greatly enlarged and hooked. Mouth slightly oblique; well-developed teeth in both jaws and on the head and shaft of the vomer, on palatines, and tongue; no teeth on the basibranchials. Branchiostegals 11–16 + 11–15; gill rakers long, serrated, slender, and closely spaced, 10–16 + 19–27; total 31–43 (usually a total of 34–42 in our area). Dorsal fin with 11–16 major rays; 13–18 major anal rays; 11–21 pectoral rays (usually 15–18 in our area); and 9–11 pelvic rays. Scales small, cycloid, pored scales in the lateral line 120–150 (usually 125–135 in our area). Vertebrae 59–72 (usually 64–72 in our area). Pyloric caeca 45–115.

Size: Sea-run sockeye may reach 84 cm (33 inches) in length and 7 kg (15.5 lb) in weight, but are usually under 76 cm (30 inches) and 5 kg (11 lb) in our area. The nonanadromous form (kokanee) are much smaller and seldom exceed 41 cm (16 inches) in length and 0.45 kg (1 lb) in weight.

Sexual dimorphism: In spawning males the upper jaw forms an elongate hooked snout with enlarged teeth, and a slight hump forms behind the head. In spawning females these characters are absent or only weakly developed.

Colour: In adults there are no distinct black spots on the back or caudal fins (kokanee sometimes have a few dark marks on the dorsal fin). At spawning time males are bright red on the back and a darker red on the sides. The underparts are dirty white. The top and upper sides of the head are green, and the snout and sides of the jaws are dusky. The dorsal, adipose, and anal fins are red, and the pectoral and pelvic fins dark with red bases. Spawning females are similarly coloured, but the red on the sides is somewhat darker.

The young have 8–12 short oval parr marks that are approximately bisected by the lateral line; the combined width of the parr marks along the lateral line is about half that of the intervening light areas. There are no dark spots on the dorsal fin. The back is a uniform bluish-green, and the sides are silvery. The fins are usually immaculate.

Distribution

In western North America from the Klamath River, California, north to Point Hope, Alaska; and in northeast Asia from northern Hokkaido north to the Anadyr River. In our area the sockeye is most abundant in the Bristol Bay region and becomes increasingly rare to the north. It does not ascend any of the large rivers (Yukon and Kuskokwim) to their headwaters. There is a nonmigratory population (kokanee) in Arctic Lake in the headwaters of the Peace River (Mackenzie system).

Taxonomic Notes

The sockeye salmon was originally described as *Salmo nerka* by Walbaum in 1792 based on the description of specimens from Kamchatka by Steller. It is now placed in the genus *Oncorhynchus,* and there are no commonly used synonyms. The kokanee (landlocked sockeye) was originally described as *Salmo kennerlyi* by Suckley in 1862. Many authors use the subspecific name *Oncorhynchus nerka kennerlyi* for the kokanee. However, there are many different populations of kokanee, undoubtedly of independent origin, that differ in gill-raker count (Nelson, 1968b) and probably in other characteristics. McCart and Anderson (1967) have shown that gill-raker counts of transplanted progeny differed significantly from those of their parents. The value of using one subspecific name to include all kokanee as distinct from all sockeye is doubtful.

Postglacial Dispersal

The distribution of sockeye includes two unglaciated areas in North America: the Bering and Pacific refuges. Sockeye probably survived glaciation in both areas, but the populations in our area were probably derived only from the Bering refuge. The Bering refuge also included parts of the Chukotsk and Kamchatka peninsulas, and the *O. nerka* populations in these regions probably had the same origin as those in our area. The populations farther south along both the Asian and North American coasts probably survived glaciation in separate refuges. The population of kokanee in Arctic Lake (upper Peace system) was probably derived from the Fraser system; several other western species have crossed the Continental Divide in this area.

Biology

The life history of sockeye salmon has been studied intensively in the Bristol Bay region of Alaska for many years, because of its relevence to fishery management. As a result there is a large body of literature on the subject, and we shall do no more than outline briefly a generalized life history. For a detailed summary of some aspects of the life history of Bristol Bay sockeye see Koo (1962).

Adult sockeye start to ascend the rivers in the Bristol Bay region in early June, and continue to run throughout July and into August. The larger runs are normally associated with river systems containing lakes. The run into the Yukon River is sporadic at best and may consist mainly of strays from more southern rivers. The farthest recorded upstream penetration of sockeye on the Yukon system is to Ruby (about 650 miles upstream). The run into the Kuskokwim system is more substantial, and penetrates about the same distance upstream (at least to Stony River). In the Bristol Bay area spawning occurs from early August to September. Most spawning is in rivers and streams tributary to lakes, but substantial numbers of fish often spawn along the lake shores in areas where ground water is percolating through gravel.

Spawning can take place over a variety of substrates, but typically the female constructs a redd in coarse gravel in a riffle area. The redd is dug by the female by turning on her side and beating with her tail. Male sockeye can occasionally be seen digging, but normally they do not aid in the excavation of the redd. There is usually a dominant male and several accessory males in attendance while the female is digging. The female is aggressive at this time and often attacks other females and attendant males. The dominant male also attacks attendant males. When the female is ready to spawn she lowers her anal fin into the nest. The dominant male swims up behind her and passes his head over her caudal peduncle several times. He then swims alongside her and quivers, both fish gape, and the eggs and sperm are shed simultaneously. The attendant males usually rush in and take part in the spawning act. The female then covers the eggs by digging upstream of the nest. A female may dig several redds and spawn with several males.

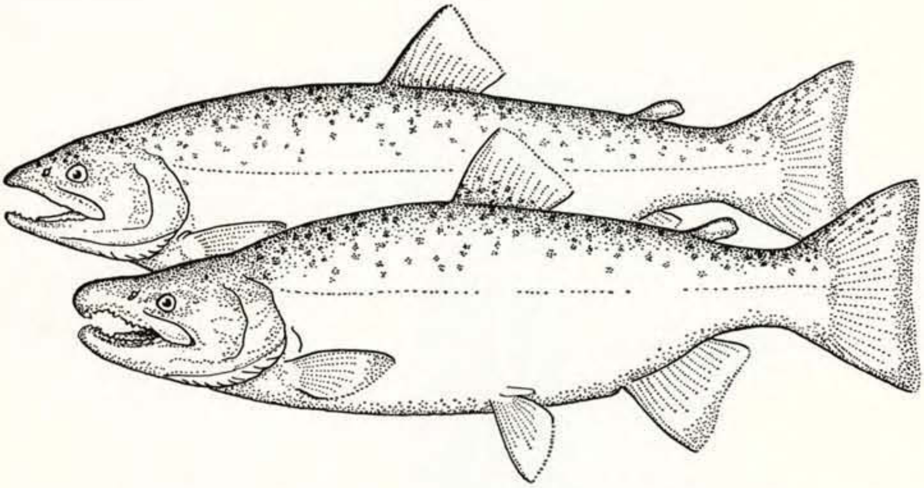
The eggs are smaller than in most other salmon (4.5–5 mm in diameter) and orange–red in colour. A large female may contain 4000 eggs. After spawning, the adults die. The eggs hatch in 6–9 weeks depending on the water temperature, and the young (alevins) remain in the gravel for 2 or 3 more weeks. The newly emerged fry then move from the stream into the lake that is associated with their spawning stream. This may involve either a downstream or an upstream movement. The fry live pelagically in the lake for 1 or 2 years before smolting and migrating to sea. During their freshwater period they live largely on planktonic animals (particularly crustaceans). The seaward migration of smolts occurs just after ice breakup. The young migrate downstream to the sea and remain at sea for 2–4 years before returning as mature adults. While at sea sockeye feed mainly on crustaceans (particularly euphausiids).

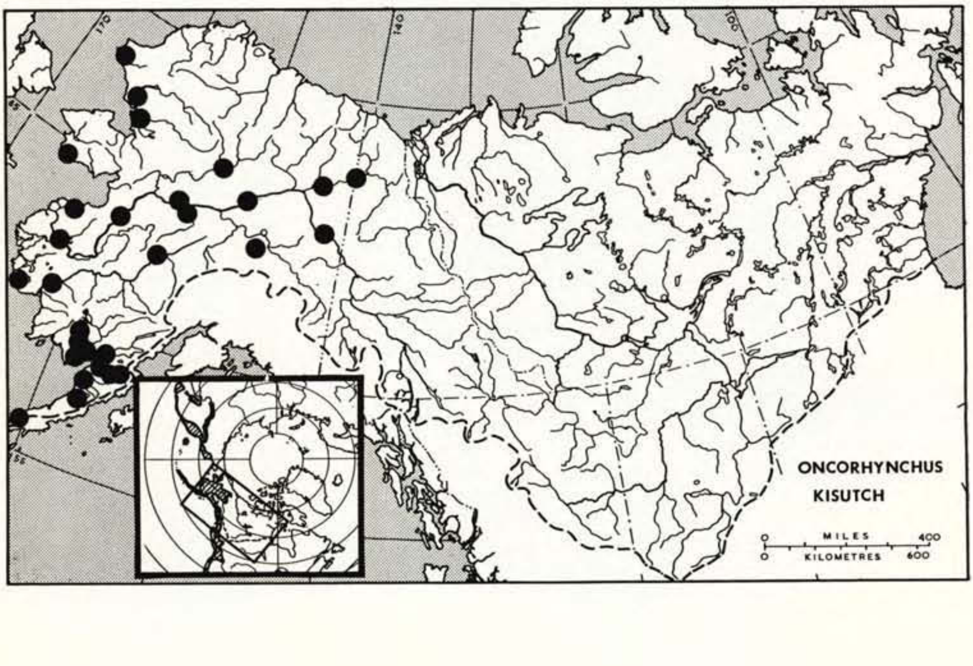
The only nonmigratory population (kokanee) of *O. nerka* we know of in our area is in Arctic Lake on the upper Parsnip River (Mackenzie system). Nothing is known about the life history of this population. We assume it is similar to kokanee populations in the Fraser system, from which it was probably derived. The life history of kokanee is similar to that of migratory sockeye except that the marine phase is omitted. Kokanee mature mainly in their 4th year but a few 3- and 5-year-old fish are usually present. Kokanee are much smaller than anadromous sockeye and are of no commercial importance in our area.

Commercially the sockeye are the most important salmon in our area. In 1964 almost 6 million sockeye worth over $6 million were taken from western Alaskan waters. This was not a particularly good year. In 1965 the run of sockeye to one Bristol Bay river system, the Kvichak River (draining Lake Iliamna), was estimated at 42.1 million fish; the commercial catch totalled 17.8 million fish. This is the largest run of sockeye ever recorded.

In contrast to its great commercial importance, the sockeye is relatively unimportant in the subsistence fishery (except in the Bristol Bay region). Sockeye are taken only occasionally by the subsistence fishery on the lower Yukon. On the Kuskokwim River in 1961 the estimated number of sockeye taken by the subsistence fishery was 54,464.

In some areas sockeye salmon are known as "red salmon," and kokanee as "little redfish," but these names are inappropriate to any but mature fish, and could be mistakenly applied to other species of salmon that develop red colouration at spawning.





ONCORHYNCHUS
KISUTCH
MILES
KILOMETRES

COHO SALMON

Oncorhynchus kisutch (Walbaum)

Kisutch is the vernacular name in Kamchatka. The French common name for this species is *saumon coho.*

Distinguishing Characters

The fine black spots on the back and upper lobe of the tail, and the absence of black pigment along the base of the teeth in the lower jaw.

Description

Body typically troutlike, somewhat compressed; head moderate (except in spawning males where the snout is greatly enlarged), about one-quarter standard length; snout rounded (the upper jaw is strongly hooked in spawning males), a little longer than the eye. Mouth large, slightly oblique; well-developed teeth in both jaws, on the head and shaft of the vomer, on the palatines, and tongue; no teeth on basibranchials. Branchiostegals 11–15 + 11–14; gill rakers rough, widely spaced, 6–9 + 12–16 (usually a total of 19–21 in our area). Dorsal fin with 9–12 major rays; 12–17 major anal rays; 13–16 pectoral rays; and 9–11 pelvic rays. Scales small, cycloid, 121–148 pored scales in the lateral line (usually 135–140 in our area). Vertebrae 61–69 (usually 65–69 in our area). Pyloric caeca 45–114 (usually 60–75 in our area).

Size: Length 96 cm (38 inches) and weight to 14 kg (31 lb) but usually about 3.6–5.5 kg (8–12 lb).

Sexual dimorphism: In spawning males the upper jaw forms an elongate hooked snout, and the teeth are enlarged. In females jaw development is less extreme.

Colour: In adults there are fine black spots on the back, dorsal fin, and upper lobe of the caudal fin. At spawning time the back and stomach become very dark, the back and head bluish green, and a brilliant red stripe develops in males. Flesh along base of teeth on lower jaw is pale.

The young have 8–12 high narrow parr marks, the highest much higher than the vertical eye diameter; the combined width of the dark areas along the lateral line less than that of the light. Pigment of adipose fin fairly uniformly distributed, the whole fin appearing dusky. The tail and most of the anal fin are reddish-orange in life. In young the first rays of the anal fin are elongate giving the fin a concave posterior margin; the leading edge of the anal fin is white, and there is usually some dark pigment behind this white stripe.

Distribution

In western North America from Monterey Bay, California, north to Point Hope, Alaska; and in northeastern Asia from Hokkaido north to the Anadyr River. Occasional specimens are taken in the sea south as far as northern Baja California. In our area the coho is abundant in the Bristol Bay region and north to the lower Yukon River, but is apparently rare north of Norton Sound. The coho ascends the Yukon River almost to the Alaska–Yukon Territory border, but has never been recorded from the Yukon Territory.

Taxonomic Notes

The coho was originally named by Walbaum in 1792 as *Salmo kisutch.* The description was based on specimens from Kamchatka described by Steller. It is now placed in the genus *Oncorhynchus.* There are no commonly used synonyms.

Postglacial Dispersal

The present distribution of the coho includes more than one unglaciated area in both Asia and North America, suggesting survival in more than one refuge. Since the Bering refuge included parts of Alaska and Siberia, coho populations on both sides of the Bering Sea are probably derived from that refuge. There has been apparently little postglacial dispersal of coho northwards from the Bering refuge. The coho probably also survived glaciation south of the Cordilleran ice sheet in North America, and south of the glaciated areas of northeast Asia. Most of the populations along the glaciated Pacific coast of North America south of the Alaska Peninsula are probably the result of postglacial dispersal from the Columbia River system.

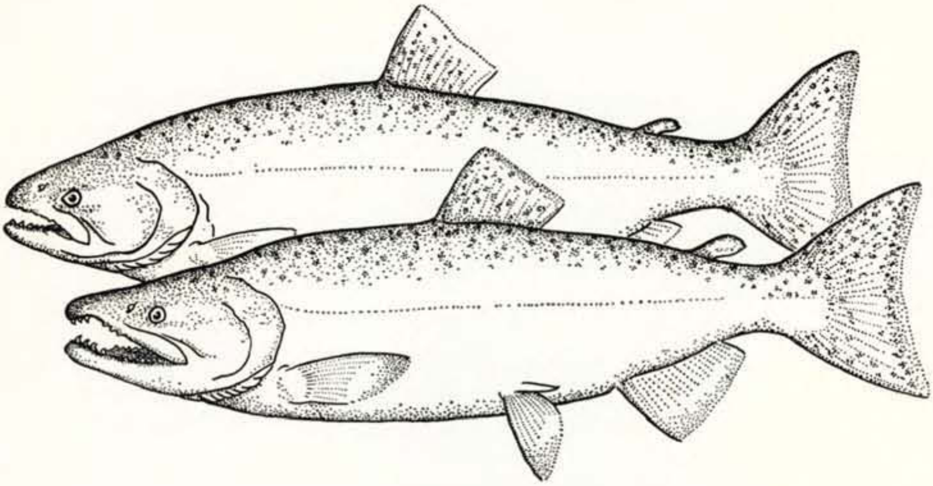
Biology

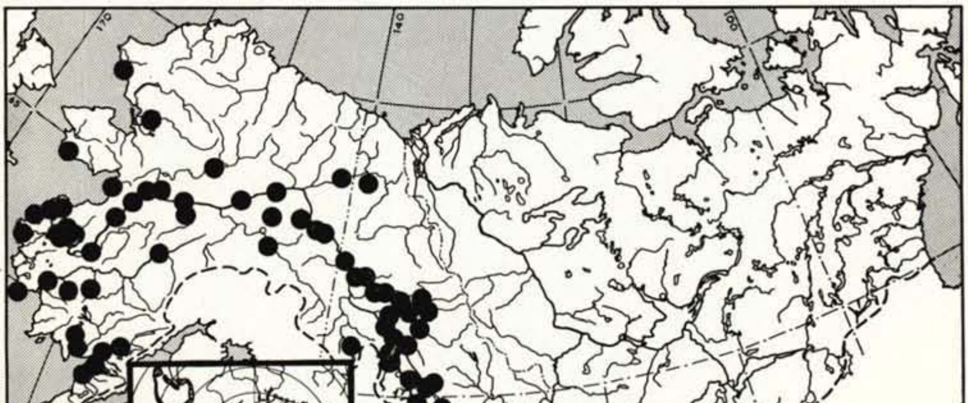
Adult coho start to ascend the rivers in our area in late June and July. They enter the Yukon River in late July but the run does not reach its peak until mid-August. Coho penetrate well upstream in the Yukon and Kuskokwim rivers. On the Yukon River coho reach the village of Woodchopper (1152 miles upstream) but apparently do not penetrate into the Yukon Territory. Runs in the Bristol Bay area are somewhat later, usually reaching a peak in August and September.

Most of the spawning occurs in November, usually in small streams tributary to larger rivers. The female digs a redd by turning on her side and beating with her tail. The nest is usually constructed in a riffle area immediately below a pool. Several males normally attend a female while she is digging the redd. One of the males is dominant and keeps the others at a distance. The female also is aggressive and attacks other females and accessory males. When the female is ready to spawn she swims across the redd and lowers her anal fin into the nest. The dominant male then swims alongside the female and quivers. Both fish gape and the eggs and sperm are shed simultaneously. The accessory males may dash in during the spawning act and also release sperm. The female covers the eggs by swimming upstream and digging above the redd. More than one male may take part in the spawning, and in southern areas precocious males (jacks) often are involved. It is not known whether jacks occur in significant numbers in the Yukon system. A female may dig several redds and spawn with several males.

The eggs are smaller than in most other salmon (4.5–6 mm in diameter) and orange–red in colour. A large female may contain 5000 eggs. After spawning the adults die. The eggs hatch in about 6–8 weeks depending on the water temperature. The young emerge from the gravel 2–3 weeks after hatching. Upon emerging the fry form small schools in shallow areas along the shores of the stream. These schools break up fairly quickly and the fry become territorial. They tend to move into pools or slow water areas where they defend territories and feed mainly on drifting insect larvae or terrestrial insects that fall into the stream. Young coho remain in streams for varying periods of time. In British Columbia the majority of young coho migrate to sea in the spring of their 2nd year. In the Yukon system most appear to remain 2 years in fresh water and migrate to sea in their 3rd year. The migratory young, called smolts, form schools and are silvery in appearance. Smolts remain inshore for their first few months in the sea, and then migrate out to the open ocean. Yukon River coho spend 2 years at sea and the returning adults range from 3 to 5 years in age. At sea they grow rapidly and feed mainly on euphausiids, squid, and small fish.

The coho is of the least value commercially of the salmons in our area. In 1964 only slightly over 100,000 fish worth about $81,000 were taken in western Alaskan waters. It is an excellent eating fish, cans well, and commands a good price, but the runs are too small in our area to make it commercially important. For the same reason it is relatively unimportant in the subsistence fishery, and is taken only incidentally in fish wheels or gillnets set for chum salmon. Along the Pacific coast it provides a considerable amount of sport fishing, in trolling and fly casting, principally in salt water. Coho have been planted in the Great Lakes with encouraging initial results, but whether this will lead to naturally reproducing populations is not yet known. Coho salmon are also known as "silver salmon," but this name is equally descriptive of some other species.




ONCORHYNCHUS
TSHAWYTSCHA
0 MILES 400
0 KILOMETRES 600

CHINOOK SALMON

Oncorhynchus tshawytscha (Walbaum)

Tshawytscha is the vernacular name in Kamchatka. The French common name for this species is *saumon chinook.*

Distinguishing Characters

The dark spotting on the back and both lobes of the tail, and the black flesh along the base of the teeth in the lower jaw.

Description

Body typically troutlike, somewhat compressed; head moderate, about one-quarter standard length except in spawning males where the snout is greatly enlarged and hooked. Mouth large, slightly oblique; well-developed teeth in both jaws, on the head and shaft of the vomer, on the palatines, and tongue; no teeth on the basibranchials. Branchiostegals 13–19 + 13–17; gill rakers rough, widely spaced, 6–10 + 10–16 (usually a total of 19–22 in our area). Dorsal fin with 10–14 major rays; 14–19 major anal rays; 14–17 pectoral rays; and 10 or 11 pelvic rays. Scales small, cycloid, 130–165 pored scales in lateral line (usually 140–150 in our area). Vertebrae 67–75 (usually 69–72 in our area). About 90–240 pyloric caeca (usually 140–200 in our area).

Size: Length 147 cm (58 inches) and weight to 57 kg (126 lb), but usually less than 101 cm (40 inches) long and less than 18 kg (40 lb) in weight.

Sexual dimorphism: In spawning males the upper jaw forms an elongate hooked snout and the teeth are enlarged. In spawning females the upper jaw is not so strongly hooked.

Colour: In adults there are black spots on back, dorsal fin, and both upper and lower lobes of the tail. At spawning time the back and sides become very dark. Flesh along the base of the teeth in the lower jaw black.

Young have 6–12 high parr marks, the highest much higher than the vertical eye diameter; dark areas along the lateral line equal to or greater than the light. Pigment of adipose fin densest around the margin, particularly at the posterior, leaving a clear "window" towards the front. No dark spots on the dorsal fin; the first rays of the anal fin are often elongate (although not as extreme as in the young of *O. kisutch*). The leading edge of the anal fin is usually white, but there is usually no dark pigment behind this stripe.

Distribution

In western North America from Ventura River, southern California, to Point Hope, Alaska; and in northeastern Asia from northern Hokkaido north to the Anadyr River. There are persistent, but unverified, reports of *O. tshawytscha* from the arctic coast of Alaska in the Point Barrow area, and from the Mackenzie Delta region. Chinook ascend the Kuskokwim and Yukon rivers to their headwaters.

Taxonomic Notes

The chinook salmon was originally named *Salmo tschawytscha* by Walbaum in 1792 based on the description of specimens from Kamchatka by Steller. It is now placed in the genus *Oncorhynchus*. There are no commonly used synonyms.

Postglacial Dispersal

The distribution of the chinook includes two unglaciated areas in North America, the Bering and Pacific refuges. The chinook salmon probably survived glaciation in both areas, but the populations in our area were probably derived only from the Bering refuge. The Bering refuge also included parts of the Chukotsk and Kamchatka peninsulas, and the *O. tshawytscha* populations in these regions probably had the same origin as those in our area. The populations farther south along the Asiatic and North American coasts probably survived glaciation in separate southern refuges.

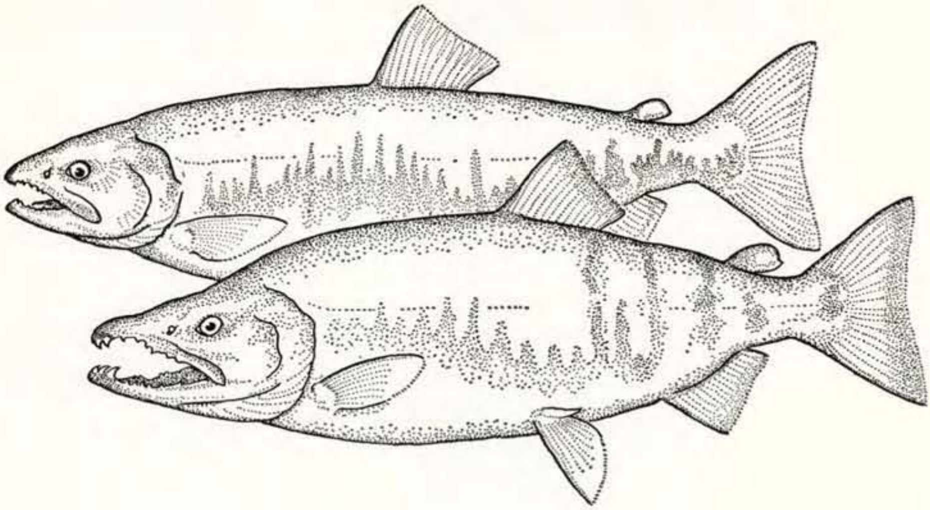
Biology

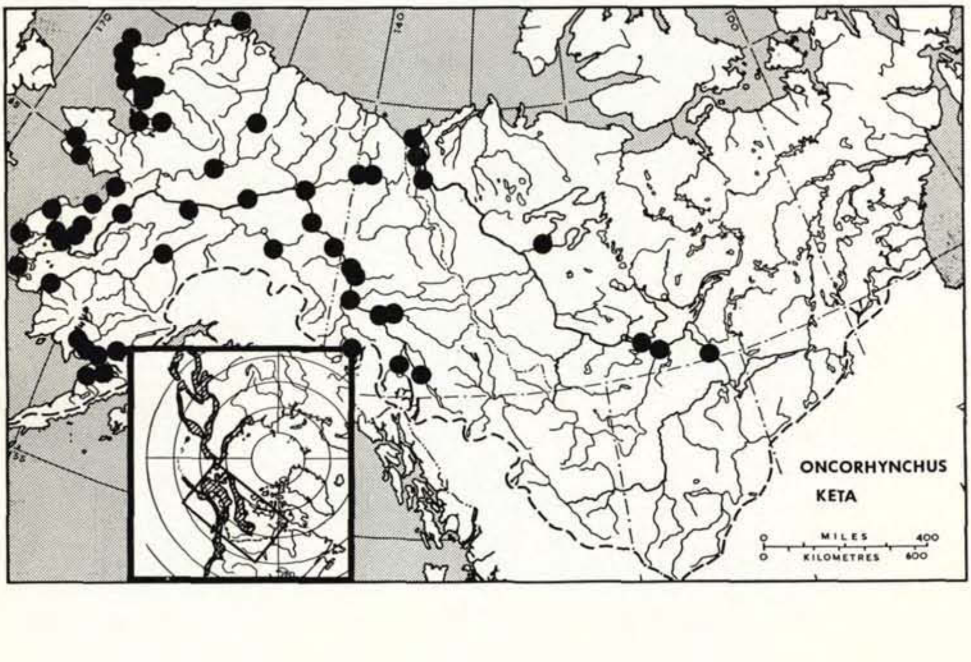
Adult chinooks start to ascend the large rivers in our area in late May and early June. The first run into the Yukon River appears in late May and the main run peaks in June. By the beginning of July the run is over except for stragglers. Chinook ascend the Yukon and Kuskokwim rivers to their headwaters. The run reaches a peak at Eagle (1256 miles up the Yukon) in mid-July and at Dawson City by late July. In the upper Yukon spawning occurs in late July and August. In the lower river spawning occurs earlier. The chinook is the largest of the Pacific salmons, and tends to spawn in larger streams over coarser gravel and in deeper water than do the other species.

The female selects the spawning site, usually a riffle area, and digs the redd by turning on her side and beating with her tail. As in other salmonids, there are usually a dominant and several accessory males in attendance. In the upper Yukon system, mature nonanadromous precocious males less than 10 cm long are occasionally taken, but it is not known whether these ever take part in actual spawning acts. When the redd is completed and the female is ready to spawn she swims across the redd and lowers her anal fin into it. The dominant male comes alongside the female and quivers. Both fish gape and the eggs and sperm are shed simultaneously. The accessory males dash in during the spawning act and also release sperm. Before spawning both the dominant male and the female are aggressive. After spawning the female digs upstream of the nest and covers the eggs. The female may dig several redds and spawn with several males.

The eggs are large (6–7 mm in diameter) and orange–red. A large female may contain up to 8000 eggs. After spawning the adults die. The eggs hatch in about 7–9 weeks depending on the water temperature. The young emerge from the gravel 2–3 weeks after hatching. The fry school at first but become territorial shortly after emerging (although not as territorial as young coho). In the Yukon system the juveniles remain 2 years in fresh water before becoming smolts and migrating to sea. During this freshwater stage they feed largely on aquatic insect larvae and terrestrial organisms that fall into the streams. Young chinooks are abundant in the small streams tributary to larger rivers like the Stewart and Pelly in the upper Yukon system. While at sea chinooks feed on euphausiids, squid, small fishes, and many other organisms. In the Yukon system females usually spend 4–5 years at sea and return to the river in their 6th or 7th year. Males mature earlier and usually spend 2–3 years at sea.

Next to sockeye salmon, chinooks are the most important commercial species in our area. On the Yukon River they are the most important commercial species. In 1964 over 260,000 chinooks worth almost $800,000 were taken from western Alaskan waters. The subsistence fishery for chinooks is also important. On the Yukon and Kuskokwim rivers in 1961 over 50,000 chinooks were taken in the subsistence fishery. Most of these were caught in fish wheels and gillnets. The bulk of the catch is dried and smoked for winter use. Chinooks are preferred as human food by the natives, and the bulk of the salmon kept for dog food are chums. Alternate common names are "spring salmon," "king salmon," and "tyee," the latter name being reserved for large fish of 30 lb or more.




ONCORHYNCHUS
KETA
MILES
KILOMETRES
0
400
0
600

CHUM SALMON

Oncorhynchus keta (Walbaum)

Keta is the Russian word for salmon. The French common name for this species is *saumon keta.*

Distinguishing Characters

The absence of distinct black spots on the back and fins, and the 11–17 smooth gill rakers on the lower limb of the first gill arch.

Description

Body typically troutlike, somewhat compressed, head moderate, about one-quarter standard length except in spawning males where the snout is greatly enlarged and hooked. Mouth large, slightly oblique; well-developed teeth in both jaws, on the head and shaft of the vomer, on the palatines, and tongue; no teeth on the basibranchials. Branchiostegals 12–16 + 12–15; gill rakers short, stout, smooth, widely spaced, 5–9 + 11–17 (usually a total of 18–21 in our area). Dorsal fin with 10–14 major rays; 13–17 major anal rays; 14–16 pectoral rays; and 10 or 11 pelvic rays. Scales small, cycloid, 124–153 pored scales in the lateral line. Vertebrae 62–71. Pyloric caeca 163–249.

Size: To 100 cm (40 inches) in length and 15 kg (33 lb) in weight, but in our area usually less than 89 cm (35 inches) long and 7.3 kg (16 lb) in weight.

Sexual dimorphism: In spawning males the upper jaw forms an elongate hooked snout and the teeth are enlarged. In spawning females the upper jaw is not strongly hooked.

Colour: In adults there are no distinct black spots on the back and fins, although fine black speckling is occasionally present. At spawning time males are dark above, dirty red on the sides, and dusky below. There are distinct greenish bars or dusky mottlings on the sides, sometimes resembling paint that has run. The colour in spawning females is similar, but the red is less pronounced.

The young have 6–14 (usually 9–12 in our area) short parr marks that rarely extend much below the lateral line. The width of the light areas is usually greater than of the dark, but the combined dark areas along the lateral line is more than half that of the light. The back is mottled green, and the sides and belly are silvery with a pale green iridescence. The fins are immaculate.

Distribution

In western North America from the Sacramento system north to Bering Strait and east to the Mackenzie River; and in northeast Asia from near Pusan, Korea, north along the Asian coast to the Arctic Ocean, and west along the arctic coast to the Lena River. In our area the chum salmon ascends the Yukon and Kuskokwim rivers almost to their headwaters, and ascends the Mackenzie River to the rapids below Fort Smith on the Slave River, and to Great Bear Lake (L. Johnson, personal communication).

Taxonomic Notes

The chum salmon was originally described as *Salmo keta* by Walbaum in 1792 based on the description of specimens from Kamchatka by Steller. It is now placed in the genus *Oncorhynchus.* There are no commonly used synonyms.

Postglacial Dispersal

The geographic range of the chum salmon includes two unglaciated areas in North America, the Bering and Pacific refuges. The chum salmon probably survived glaciation in both areas, but in our area were probably derived only from the Bering refuge. The Bering refuge also included the Chukotsk and Kamchatka peninsulas; *O. keta* populations in these regions and in arctic Siberia probably had the same origin as those in our area. The *O. keta* populations farther south along the Asian coast may have survived glaciation in a southern refuge (Amur River?). The only significant postglacial dispersal of *O. keta* from the Bering refuge has been east and west along the arctic coasts of Siberia and North America.

Biology

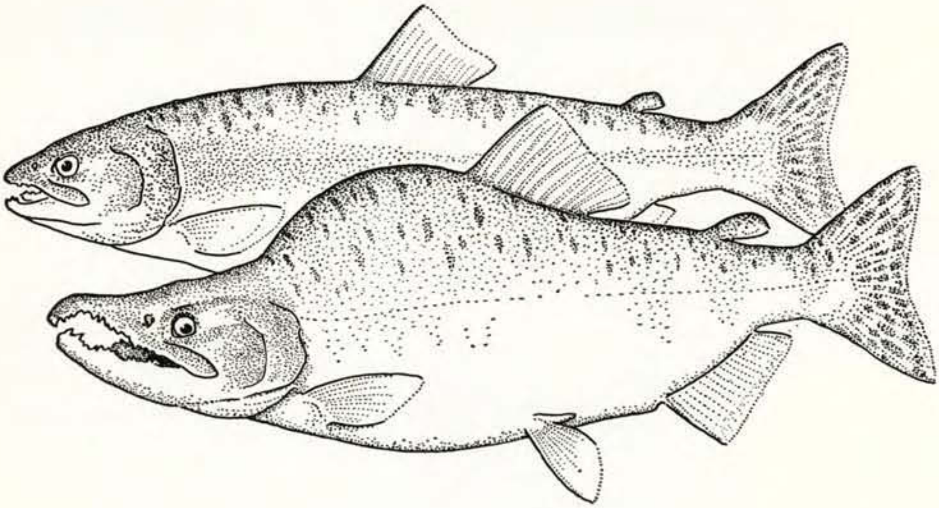
Like the pink salmon, the chum salmon spends very little time in fresh water. In our area, adults start to ascend the rivers in early July (the first run into the Yukon River usually appears in early June, other runs follow later). Chum salmon penetrate large rivers such as the Yukon and Kuskokwim right to their headwaters. They also ascend the Mackenzie River to above Great Slave Lake. The main run of chum salmon passes Eagle (1256 miles up the Yukon River) in early September and reaches Dawson City a week or so later. Spawning in the upper tributaries of the Yukon system occurs in late September. In the lower Yukon spawning occurs in early

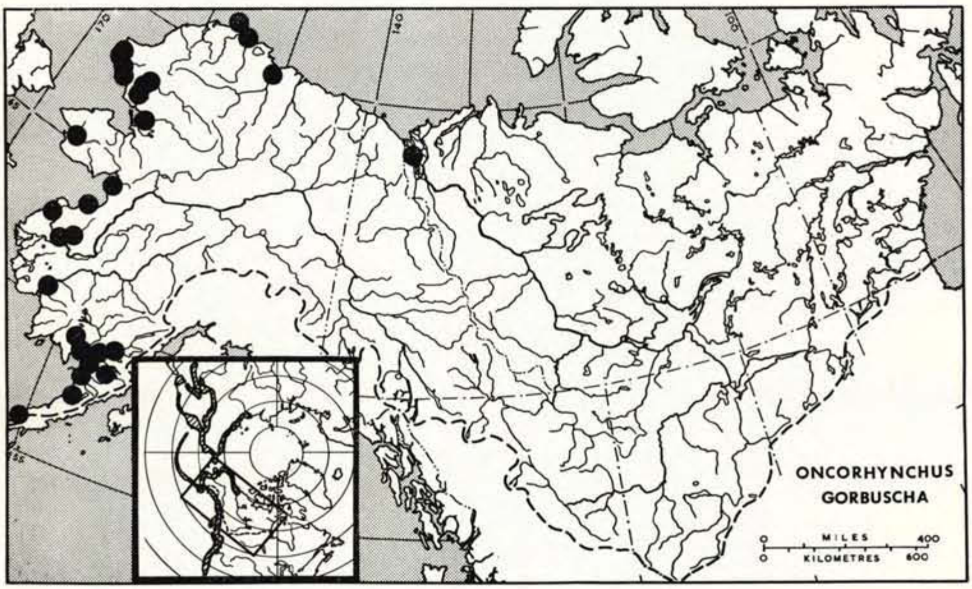
July. The first chums appear at the mouth of the Mackenzie River in August and reach Great Slave Lake in late September or October.

Spawning occurs over a variety of substrates, usually in riffle areas with gravel size similar to that used by pink salmon, but also in coarser gravel and even in bedrock areas over loose rubble. The female builds a nest by turning on her side and beating with her tail. There is usually a dominant and several accessory males present. When a female is ready to spawn she swims over the redd and lowers her anal fin into the nest. This apparently stimulates the attending males. The dominant male comes alongside the female and quivers violently. Both fish gape and the eggs and sperm are shed simultaneously. The female covers the eggs by swimming upstream and digging above the redd. A female may dig several redds and spawn with several males. Males may spawn with several females.

The eggs are large (about 6–7 mm in diameter) and orange–red. A large female may contain as many as 4000 eggs. After spawning the adults die. The egg development is dependent upon water temperature; in British Columbia hatching usually occurs between December and February. It is not known when hatching occurs in our area. The alevins remain in the gravel for several weeks after hatching. When the young emerge from the gravel they begin a downstream migration (usually at night). In the large northern rivers this downstream migration must take a considerable period of time and the young must feed along the way. As a result the young chum salmon leaving these rivers should be considerably larger than typical downstream migrants in more southern areas. The fry apparently school in estuarine areas and are tolerant of salt water. The young remain near shore for several months and then move out to sea. Yukon River chums remain at sea for 3–5 years before maturing and returning to the river. At sea they feed mainly on copepods, amphipods, and euphausiid shrimp. As they grow larger they also take squids and small fishes.

Chum salmon are of considerable importance commercially. In 1964 over 1 million chum salmon worth over $600,000 were taken in western Alaskan waters. Although the chum salmon is not as important in terms of dollars as some other species, it is undoubtedly the most important of the salmons in the economy of the native peoples of the large northern rivers. On the Yukon and Kuskokwim rivers large numbers of chums are taken annually by the subsistence fishery. They are caught primarily in fish wheels and gillnets, and are dried for winter use for either human or dog food. North of the Yukon system chum are the only salmon taken in any numbers. In the Mackenzie system the runs are too small to support a fishery, and the few taken each year are caught incidentally in whitefish nets. Chum salmon are sometimes called "dog salmon."




ONCORHYNCHUS
GORBUSCHA
MILES
400
KILOMETRES
600

PINK SALMON

Oncorhynchus gorbuscha (Walbaum)

Gorbuscha is the Russian name for humpback. The French common name for this species is *saumon rose*.

Distinguishing Characters

The large black spots on the back, the dark, elongate, oval blotches on both lobes of the tail, and the 16–21 gill rakers on the lower limb of the first gill arch.

Description

Body typically troutlike, somewhat compressed; head moderate, about one-quarter standard length except in spawning males where the snout is greatly enlarged and hooked. Mouth slightly oblique; well-developed teeth in both jaws and on the head and shaft of the vomer, on palatines, and tongue; no teeth on the basibranchials. Branchiostegals 10–15 + 10–15; gill rakers moderate, 8–14 + 16–21 (usually a total of 28–32 in our area). Dorsal fin with 10–16 major rays; 13–19 major anal rays; 14–17 pectoral rays; and 9–11 pelvic rays. Scales small, cycloid, 147–198 pored scales in the lateral line. Vertebrae 63–72. About 95–224 pyloric caeca (usually 130–160 in our area).

Size: Length 76 cm (30 inches) and 6.3 kg (14 lb) in weight, but usually less than 61 cm (24 inches) in length and 2.7 kg (6 lb) in weight in our area.

Sexual dimorphism: In spawning males the snout becomes elongate and hooked, the teeth enlarge, and a prominent hump forms behind the head. In spawning females these characters are absent or developed only weakly.

Colour: In adults there are large black spots on the back, adipose, and both lobes of the caudal fin. The spots on the caudal fin are oval, and the largest are at least as large as the eye diameter. At spawning time males become dark on the back and red on the sides. There are also usually brown–green blotches on the sides. The colours in spawning females are less distinct.

The young are without parr marks, and have no dark spots on the dorsal fin. They are bluish-green on the back and silvery on the sides. The membranes of the dorsal and caudal fins are often dusky.

Distribution

In Northeast Asia from Peter-the-Great Bay north to Bering Strait and then west to the Lena River; in western North America from the Sacramento River, California, north to Bering Strait and then east to the Mackenzie River. In our area it ascends large rivers only short distances.

Taxonomic Notes

The pink salmon was originally described as *Salmo gorbuscha* by Walbaum in 1792 based on the description of specimens from Kamchatka by Steller. It is now placed in the genus *Oncorhynchus*. There are no commonly used synonyms.

Postglacial Dispersal

The geographic range of the pink salmon includes two unglaciated areas in North America, the Bering and Pacific refuges. Pink salmon probably survived glaciation in both areas, but the populations in our area were probably derived only from the Bering refuge. The Bering refuge also included the Chukotsk and Kamchatka peninsulas, and populations in these regions and in arctic Siberia probably had the same origin as those in our area (this suggestion is supported by the work of Amos et al., 1963). The *O. gorbuscha* populations farther south along the Asian coast may have survived glaciation in a southern refuge (Amur River?). The only significant postglacial dispersal from the Bering refuge has been east and west along the arctic coasts of Siberia and North America.

Biology

The pink salmon spends very little time in fresh water. In our area the adults start to ascend the rivers and streams from mid-June to late September. They do not move far upstream, and even in such large rivers as the Yukon and Kuskokwim seldom penetrate more than 160 km (100 miles) upstream. Most spawning is in small streams over walnut-sized gravel in water about 1 ft (30 cm) deep and of moderate velocity. Some populations spawn in intertidal areas. Although pink salmon may enter a river in late June, spawning usually occurs in August and September (mid-July on the lower Yukon).

The female digs a redd in the gravel, usually in a riffle area, but occasionally just below a pool. The female digs the redd by turning on her side and beating with her tail. While the female is digging there may be some aggressive behaviour between the males in attendance and the female may also be aggressive before spawning. Usually only the dominant male actually fertilizes the eggs, but up to six males have been recorded spawning with a single female (Wickett, 1959). When the female is ready to spawn she swims slowly over the redd and lowers her anal fin into the nest. The male then comes alongside and quivers violently. Both fish gape and the eggs and sperm are shed simultaneously. The female covers the eggs by swimming upstream and digging above the redd. A female may dig several redds and spawn with several males.

The eggs are large (about 6 mm in diameter) and orange–red. A large female may contain as many as 2000 eggs. After spawning the adults die. The developmental period is affected by water temperature, but hatching usually occurs from December through February. The alevins remain in the gravel for several weeks and emerge in April and May. The fry migrate downstream immediately after hatching, migrating at night and hiding in the gravel by day. Migratory fry usually do not feed, but if the distance is great they feed on larval insects. Fry form large schools in estuarine areas and remain there for several months before migrating out to sea. The fry are euryhaline and can osmoregulate in sea water (Weisbart, 1968). Pink salmon have a 2-year life cycle (3-year-old fish are extremely rare). At sea they feed mainly on euphausiids, amphipods, copepods, squid, and small fish. Many streams in which pink salmon spawn contain spawning fish every year. Since they have a 2-year life cycle there must be relatively little interbreeding between odd and even year populations.

Most of the above information on pink salmon is summarized from work in southeastern Alaska and British Columbia. There is very little known about more northern and arctic populations, and in these areas the life cyle of pink salmon may differ in some ways from the southern populations. For example, in the Wood River system in the Bristol Bay area of Alaska occasional pink salmon fingerlings are taken in fresh water in September that average 89 mm in length. It is not known whether these fish overwinter in fresh water before going to sea (R. L. Burgner, personal communication).

In our area pink salmon are abundant in the Bristol Bay area of Alaska, and extend farther north than other species (except the chum). The North American catches of pink salmon are smaller than the Asian catches, but are still of considerable commercial value. In 1964 almost 2 million pink salmon worth about $500,000 were taken from western Alaskan waters. Pinks are less important to native peoples as a food source than are chum, coho, and chinook salmon, and relatively few are taken in the subsistence fishery. In some areas they are known as "humpback salmon."

THE SMELTS — Family OSMERIDAE

The smelts are small, elongate, silvery fishes with teeth in the jaws, a single soft dorsal fin, an adipose fin, and no fleshy appendage at the pelvic base. The stomach is distinctive, having usually a blind sac, and few or no pyloric caeca. Some smelts live entirely in fresh water, some live in the sea but enter fresh water to spawn, and some live and reproduce in the sea. The males, which are usually smaller than females at maturity, frequently have longer paired fins and may develop tubercles or special enlarged scales before spawning. The eggs are small and adhesive. Smelts may occur in large schools. Many are rich in oil and are excellent food fishes.

Smelts are found in temperate and cold waters of the northern hemisphere. There are 6 genera and 10 species, 4 of which enter our area.

KEY TO THE SPECIES

1(2) Mouth small, extending back to anterior margin or middle of pupil; pyloric caeca 0–3 .... Pond smelt, *Hypomesus olidus* (Pallas) (p. 201)

2(1) Mouth large, extending back to the posterior margin of pupil; pyloric caeca 4–12 3

3(4) Lining of body cavity black; strong striations on gill covers .... Eulachon, *Thaleichthys pacificus* (Richardson) (p. 197)

4(3) Lining of body cavity colourless or silvery; striations on gill covers weak or absent 5

5(6) Pectoral fins about equal to head length; origin of dorsal fin behind origin of pelvic fins (Fig. 19A) .... Longfin smelt, *Spirinchus thaleichthys* (Ayres) (p. 189)

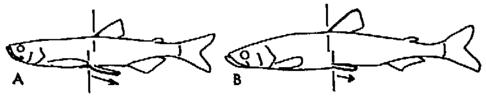
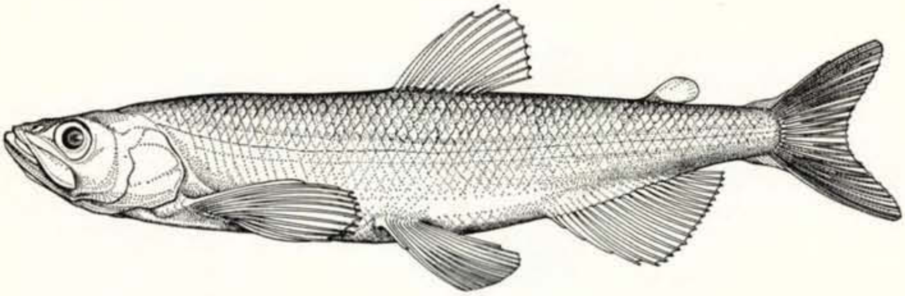
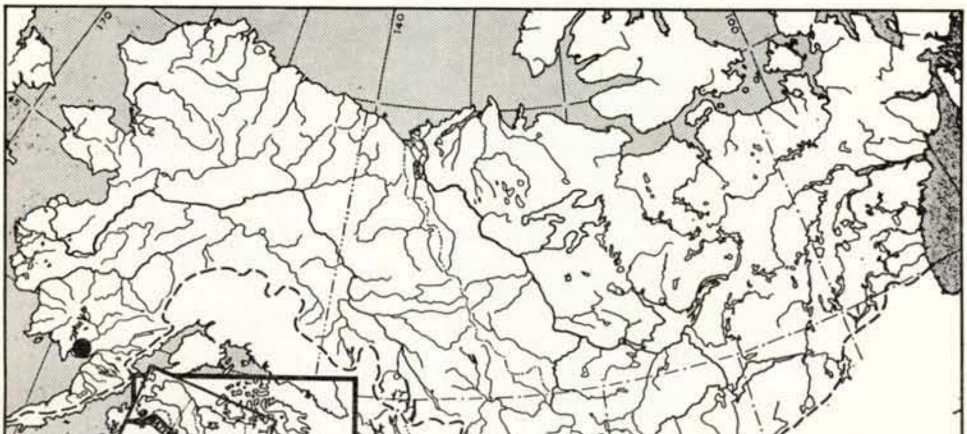


Fig. 19. Lengths of pelvic fins, and their position relative to dorsal fin. A, *Spirinchus thaleichthys*; B, *Osmerus eperlanus*.

6(5) Pectoral fins much shorter than head length; origin of dorsal fin slightly in front of origin of pelvic fins (Fig. 19B) .... Boreal smelt, *"Osmerus eperlanus"* complex (p. 193)




170
140
100
SPIRINCHUS
THALEICHTHYS
0 MILES 400
0 KILOMETRES 600

LONGFIN SMELT

Spirinchus thaleichthys (Ayres)

Spirinchus is probably from the Dutch word *"spiering"* for smelt and *thaleichthys* is from the generic name of the similar-tasting eulachon. The French common name for this species is *éperlan d'hiver*.

Distinguishing Characters

The large mouth, long pectoral fins almost reaching the origin of the pelvics, and lack of strong striations on the gill cover.

Description

Body elongate, compressed, head short, about one-quarter standard length; eye moderate, about equal to snout. Mouth large, oblique, extending to or past posterior margin of pupil in adult (shorter in young); small teeth in both jaws, on tongue, vomer, palatine, pterygoid, and basibranchial bones. Some specimens have a few weak striations on the opercle. Branchiostegals 7–8; gill rakers long and slender, 10–13 + 27–34. Dorsal fin with 8–10 major rays; 15–19 major anal rays (usually 16–18); 10–12 pectoral rays; and 8 pelvic rays. Pectoral fin length about equal to head length; pectoral tip reaching nearly opposite to base of pelvic fin. Scales moderate, cycloid; lateral line incomplete, with 14–21 pored scales; midlateral scales 54–63 (57–62 in Alaska). Vertebrae 55–61 (58–61 in Alaska). Pyloric caeca 4–6.

Size: Usually to about 150 mm (6 inches) total length, rarely to 200 mm (8 inches).

Sexual dimorphism: First ray of paired fins and rays of median fins enlarged and stiffened in males. Spawning males have small tubercles developed on the head and paired fins; the leading edge of the dorsal fin becomes rough, a narrow ridge develops along the lateral line, and the base of the anal fin develops a broadened shelf. Tubercles are usually absent in females.

Colour: Adults are dusky on the back and silvery below. The fins are usually stippled along the rays but the membranes are immaculate. Young (up to 70 mm) are translucent.

Distribution

On the west coast of North America from San Francisco Bay, California, to Bristol Bay, Alaska. Recorded on the Pacific coast as far north as the south side of the Alaska Peninsula (Wide Bay), but so far taken in our area only from Nushagak River on Bristol Bay (Gilbert, 1895). Occurring in fresh waters only in rivers close to the sea, except for apparently nonmigratory populations in Harrison Lake in the lower Fraser River valley and Lake Washington near Seattle.

Taxonomic Notes

The longfin smelt was first described as *Osmerus thaleichthys* from San Francisco by Ayres in 1860. Taxonomy of the species has been reviewed by McAllister (1963), who showed that *Spirinchus dilatus* Schultz and Chapman is a synonym. Vertebral and scale counts are said to increase from south to north in clinal fashion, although Dryfoos (MS, 1965) has shown that the nonmigratory population in Harrison Lake, British Columbia, have vertebral counts similar to those of California fish.

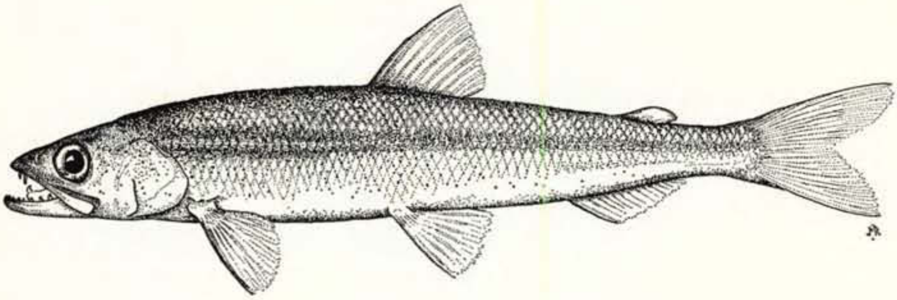
Postglacial Dispersal

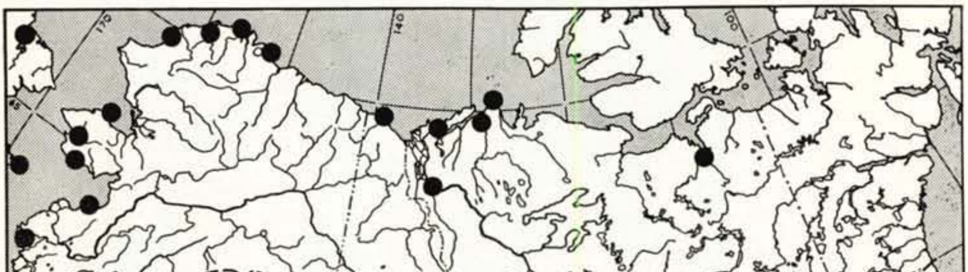
Its southern distribution suggests that the longfin smelt survived glaciation south of the Wisconsin ice sheet on the Pacific coast and has since spread northward. The Bristol Bay record suggests the possibility of a second northern refuge, but the species might be expected to have a wider distribution in the Bering area if a centre of colonization had persisted there throughout glaciation.

Biology

Except for nonmigratory populations in Harrison Lake and Lake Washington (Dryfoos, MS, 1965), the longfin smelt is anadromous. In the sea in British Columbia waters it inhabits depths from 10 to 70 fathoms and is captured frequently during winter months, particularly by shrimp trawls that encounter the schools accidentally (Clemens and Wilby, 1961). Food of young includes the shrimplike *Neomysis*; larger fish feed on euphausiids, copepods, and Cumacea (McAllister, 1963). The nonmigratory populations feed almost exclusively on zooplankton, largely *Neomysis*.

In the southern half of their range most longfin smelts mature in their 2nd year regardless of their size at this time (Dryfoos, MS, 1965). Only a very few fish survive after spawning; those surviving to be 3 years old are predominately females. Anadromous British Columbia populations spawn from October to December in streams near the sea. Spawning in Lake Washington tributaries extends from mid-December through mid-February. Females of about 120 mm standard length have about 18,000 eggs. Preserved eggs of mature fish are about 1.0 mm in diameter. Dryfoos (MS, 1965) hatched eggs after 40 days at 44.5 F (7 C). Newly hatched larvae were between 7 and 8 mm long. The flesh of the longfin smelt has a fine flavour, but it is soft and does not keep well.




"OSMERUS
EPERLANUS"
COMPLEX
MILES
KILOMETRES
EPERLANUS
DENTEX
MORDAX

BOREAL SMELT

"Osmerus eperlanus" complex including *Osmerus eperlanus* (Linnaeus)

Osmerus means *odorous* (from Greek *osme* for smell or scent) and *eperlanus* is probably from the French word for smelt. The French common name for this species is *éperlan du nord.*

Distinguishing Characters

The large mouth, short pectoral fins, lack of striations on the gill cover, and large canine teeth.

Description

Body elongate, compressed; head moderate, usually a little more than one-quarter standard length, eye moderate, less than snout length. Mouth large, oblique, extending back to posterior margin of pupil in adult; well-developed teeth in both jaws, and on the palatine, pterygoid, and basibranchial bones; canine teeth on the tongue and vomer. Branchiostegals 7–8 (rarely 6); gill rakers long and slender, 7–11 +18–24 (usually 8–10 + 19–22 in our area). Dorsal fin with 7–11 major rays (8–10 in our area); 11–16 major anal rays (12–16 in our area); 11–14 pectoral rays; and 8 pelvic rays. Length of pectoral fin much shorter than head length; pectoral tip reaching one-half to two-thirds distance to pelvic base. Origin of pelvic fins behind origin of dorsal fin. Scales moderate, cycloid, 0–30 pored scales (usually 17–25 in our area but some with less than 14) in the incomplete lateral line; 62–72 midlateral scales. Vertebrae 58–70 (usually 63–67 in our area). Pyloric caeca 3–9 (5–9 in our area).

Size: Up to 40 cm (15.7 inches) in total length, but usually under 25 cm (10 inches).

Sexual dimorphism: Large tubercles form on the scales, and smaller ones on the head and fins, of spawning males. A slight lateral ridge is also developed in spawning males. In females the paired fins are shorter, and spawning tubercles are poorly developed.

Colour: Adults are a light olive green on the back and an iridescent silver below. There is a dark band along the lateral line evident in preserved specimens, and usually a dark blotch showing through the operculum. The fins are normally immaculate, but some of the fin rays may have dusky speckling on them. Young specimens are somewhat translucent.

Distribution

In North America, on the Atlantic coast from Virginia north to Labrador, on the Pacific coast from Barkley Sound on Vancouver Island north to Yakutat, and on Bering Sea and Arctic Ocean coasts from Bristol Bay to Cape Bathurst. On St. Lawrence Island, Bering Sea. In Eurasia, from Wonsan, Korea, north to Bering Strait, including Hokkaido and Sakhalin, and west along the arctic coast to the White Sea; a somewhat different form ranges south in Europe from the Baltic sea to the Loire River in France.

Taxonomic Notes

This is a wide-ranging fish that has been subdivided into subspecies by some and into several distinct species by others. Linnaeus named it *Salmo eperlanus* in 1758, from European seas and rivers. The eastern North American form has been called *Osmerus mordax,* and the Pacific form of Asia and western North America *O. dentex.* McAllister (1963) unites all these into one species with two subspecies, *O. eperlanus eperlanus* of the Baltic and North Sea drainages, and *O. eperlanus mordax* (which usually has 14 or more pored lateral line scales) throughout the rest of the range. He found 94% separation between *"dentex"* and *"mordax"* samples on the basis of vertebral count, but felt that available data were insufficient to distinguish subspecies. We find, from somewhat larger samples, that populations from eastern and western North America can be separated slightly more sharply than this, either on vertebral or pyloric caecal count. We also find that several specimens from Alaska and Northwest Territories have fewer than 14 pored lateral line scales, which tends to break down the distinction of the Baltic form to which McAllister gives subspecific rank. Moreover, there are growing suspicions that two "biological" species of *Osmerus* may live sympatrically in Sweden, in Quebec, and in New England. Our conclusion is that *Osmerus* probably forms a systematic complex which is not yet understood; for the present it is best to apply the term *"Osmerus eperlanus"* complex until we are more informed.

Postglacial Dispersal

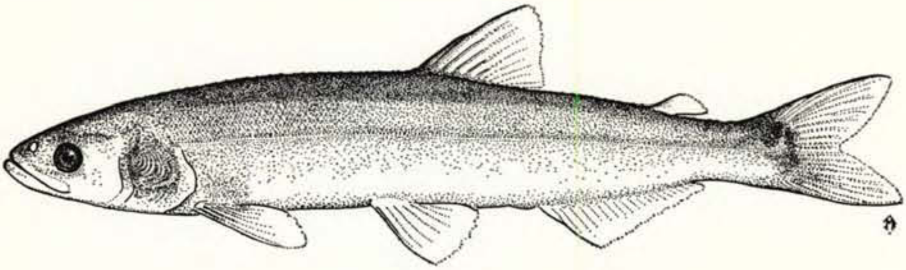
The gap in northern distribution, and the moderate morphological divergence between fish on either side of it, suggest that North American boreal smelt survived glaciation in at least two refuges, one on the Atlantic coast and one in the Bering region. Probably several refuges were involved in the circumpolar range of the "species." Ability to survive in either landlocked or anadromous form, coupled with toleration of periglacial conditions, has probably produced a complex of forms grading from slightly differentiated races to sympatric species. Their postglacial dispersal routes cannot be understood until their phylogeny has been unravelled.

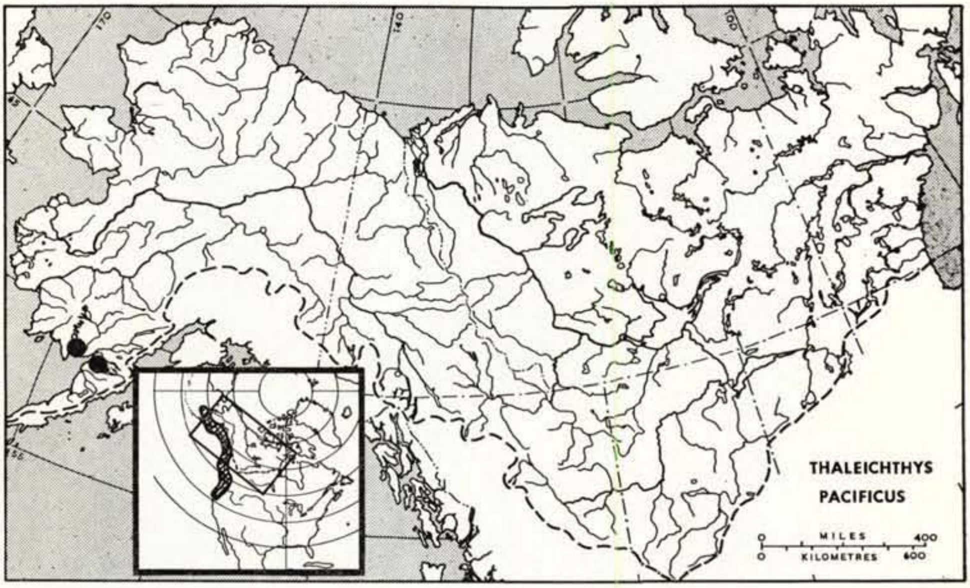
Biology

Boreal smelt are anadromous in some places, but landlocked races occur throughout many parts of their range. They have been introduced into the upper Great Lakes and there have become enormously abundant. Adults feed partially on crustaceans and, as is suggested by their large canine teeth, on small fish. In the Yenisei River of Siberia boreal smelt first spawn in the 3rd or 4th year of life, and may live at least 8 years. They ascend the Yenisei as much as 1000 km (624 miles), moving upstream before the ice has broken, and spawning in May or June. Eggs are shed over stones or gravel, not mud. In anadromous races, the young probably drop down to sea during their first summer.

This species supports fisheries in many places; it is caught in midwater trawls in the Great Lakes, it is subject to commercial exploitation in some Arctic rivers in the USSR, and was at one time an important part of the food of natives in Bristol Bay. It is variously fished by fyke nets, dipnets, and fine mesh gillnets, and may be angled or otherwise caught through holes in the ice.

Professor Seeley (1886) wrote that "the name Smelt is said to be derived from the odour which this fish exhales when freshly taken from the water, an odour which is not always the same, but is usually suggestive of cucumber, though Pennant also compares it to violets. In Germany the perfume would appear to be stronger, since Benecke says the Smelt has a frightful smell of putrid cucumbers." A former local German name was *Stinkfisch*. In England smelt used to be split and dried, and "was thus considered to add a particular relish to the morning dram of spirits." Frozen smelt from the Great Lakes are marketed commercially. Kendall (1927) says of the species in eastern America that when perfectly fresh, and fried after rolling in corn meal or cracker crumbs, it is one of the most delicious of pan fishes.




THALEICHTHYS
PACIFICUS
0 MILES 400
0 KILOMETRES 600

EULACHON

Thaleichthys pacificus (Richardson)

Thaleichthys means *rich fish* (referring to high oil content) and *pacificus* means *of the Pacific.* The French common name for this species is *eulakane.*

Distinguishing Characters

The large mouth, short pectoral fins, and the concentric striations on the gill cover.

Description

Body elongate, compressed; head short, less than one-quarter standard length; eye small, about one-half snout length. Mouth large, oblique, extending to or past posterior margin of orbit in adults; small teeth in both jaws, on tongue, palatine, pterygoid, and basibranchial bones; two moderate canines on the vomer (usually lost in spawning fish). Strong concentric striations on opercle and subopercle. Branchiostegals 7–8 (rarely 6); gill rakers long and slender, 4–6 + 16–18 in our area (13–18 elsewhere). Dorsal fin with 10–12 major rays (rarely 13); 18–23 (usually 20 or 21 in our area) major anal rays; 10–12 (usually 11) pectoral rays; and 8 pelvic rays. Pectoral shorter than head, the tip reaching about two-thirds the distance to the pelvic base. Scales small, cycloid, 70–86 pored scales in the complete lateral line. Vertebrae 65–72. Pyloric caeca long, 8–12 (usually 10 or 11).

Size: To 300 mm (about 12 inches) in total length.

Sexual dimorphism: In spawning males there is a distinct midlateral ridge, and well-developed tubercles on the head, scales, and fins. In females the tubercles are not well developed. The pelvic fins in males often reach the anus; they are much shorter in females.

Colour: Adults are brown to bluish-black on the back and head and a dark blotch shows through the gill cover. The lower surfaces are whitish, and the fins are usually immaculate, although the caudal and pectoral fins are often dusky.

Distribution

On the west coast of North America from Klamath River, California, north to the eastern Bering Sea. In our area, from Nushagak River (Gilbert, 1895) and Bristol Bay; also taken in Bering Sea 130 miles north of Unimak Pass, and from Pribiloff Islands.

Taxonomic Notes

The eulachon was first named *Salmo (Mallotus) pacificus* from the Columbia River by Richardson in 1836. This is the only species currently recognized in the genus *Thaleichthys.*

Postglacial Dispersal

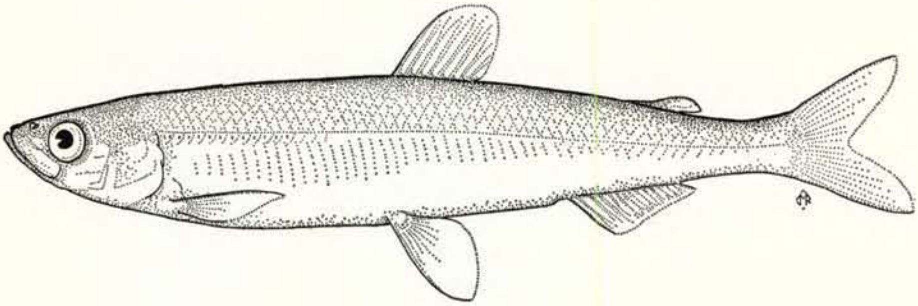
Eulachons apparently survived glaciation south of the ice sheet along the Pacific coast of North America. Because of their restricted occurrence north of the Alaska Peninsula, it seems more probable that they have entered the eastern Bering Sea from the south postglacially, rather than that they have survived glaciation in a refuge at the northern end of their present range.

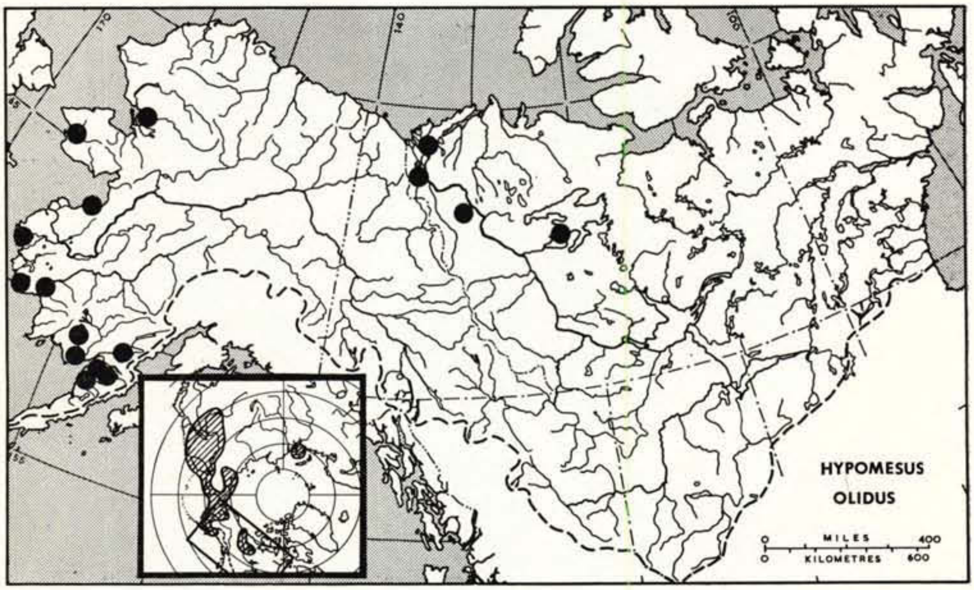
Biology

Eulachons are anadromous fish that penetrate coastal rivers only a few miles at spawning time. Most of their life is spent in inshore marine waters; larvae and juveniles may spend much of their first 2 years of life in the echo-scattering layer feeding on euphausiid shrimps (Barraclough, 1964).

Contrary to earlier beliefs, eulachons in British Columbia waters do not spawn until they are 3 years of age, and a few survive spawning and may return to spawn in a subsequent year (Barraclough, 1964). Spawning runs occur in British Columbia from March to mid-May. Females produce about 25,000 eggs, which are shed over sand or gravel. The outer of the two egg membranes is fragile and breaks upon contact with the bottom, to which it adheres. The inner membrane remains attached to the outer at one point, so the egg is held up from the bottom on a little stalk. The larvae hatch at a length of 4–5 mm, and are carried out to sea shortly after emerging.

In the sea, eulachons form part of the food of salmon and of seals, and during the spawning runs may be eaten in immense quantities by sturgeon. In fresh water they are taken by man for the fresh-fish market, having an oily but attractive flavour, or for feed for fur-farm animals. They were once important to Indians for food and as a source of oil; "eulachon" is a Chinook jargon name, and the alternative name "candlefish" arises from the fact that the dried fish can be burned.





HYPOMESUS
OLIDUS
MILES
400
KILOMETRES
600

POND SMELT

Hypomesus olidus (Pallas)

Hypomesus means *below the middle* (referring to position of pelvic fins) and *olidus* means *oily*. The French common name for this species is *éperlan à petite bouche*.

Distinguishing Characters

The small mouth, absence of large canine teeth, and large scales.

Description

Body robust in adults, somewhat compressed laterally; head short, more than 4 times in standard length; eye moderate, the horizontal diameter usually a little greater than snout length. Mouth small, oblique, extending back to anterior margin or middle of pupil; small teeth in both jaws, on the tongue, and on the vomer, palatine, pterygoid, and basibranchial bones. Branchiostegals 5–8 (6–7 in our area) on both sides; gill rakers long and slender, 8–12 + 17–22. Dorsal fin with 7–10 major rays; 12–18 major anal rays (in our area 12–16); 10–12 pectoral rays, usually 11; and 8 pelvic rays. Pectoral shorter than head, the tip reaching 40–80% of distance from pectoral to pelvic bases. Scales large, cycloid; lateral line incomplete, with 7–16 pored scales; 51–62 midlateral scales. Vertebrae 51–62. Pyloric caeca 0–4 (usually 2 in our area).

Size: Usually under 150 mm (about 6 inches) in total length, but rarely up to 200 mm (8 inches). The population in the Woods River system mature at about 75 mm.

Sexual dimorphism: In mature males the pelvic fins almost reach the anus; pelvics are much shorter in mature females. There are well-developed tubercles on the head, scales, and fins of spawning males. These tubercles are usually absent on females, but may occasionally be weakly represented.

Colour: Adults are light brown to olive green on the back with a metallic silver band along the midlateral line, and silvery white on the ventral surface. All fins are immaculate. The young are similarly coloured but the metallic silver stripe is less pronounced.

Distribution

In Asia, south to the Tartary Strait and a few lakes in northern Hokkaido; north to Chukotsk; west on the arctic coast to Alazeya River in Siberia, with an isolated population farther west in Lake Krugloe, Kara Sea drainage. In North America, from Copper River on Gulf of Alaska, many localities on the Alaskan coast of Bering Sea, and north to Kobuk River. Also in Mackenzie River upstream as far as Great Bear Lake.

Taxonomic Notes

The pond smelt was named *Salmo (Osmerus) olidus* from Kamchatka by Pallas in 1811. It has been erroneously reported from California, but McAllister (1963) has shown this to be a distinct species *Hypomesus transpacificus,* which occurs also around the Sea of Japan (Klukanov, 1966). Although arctic specimens tend to have shorter pectorals than do Pacific specimens, overlap is too great to warrant subspecific designations (McAllister, 1963).

Postglacial Dispersal

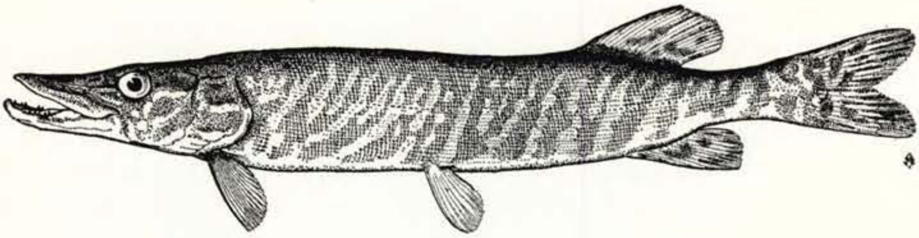
The pond smelt apparently survived glaciation north and west of the North American Wisconsin ice sheet. Judging from its present distribution the species may have persisted either north or south of the Bering land bridge, perhaps both, and also perhaps well south on the Asian side of the Pacific Ocean. The Lake Krugloe population in Siberia lies 1700 miles west of the nearest other known Siberian population, suggesting that an additional glacial refuge may have existed in the Kara Sea area. Further study may disclose slight genetic differences related to different refuges from which the pond smelt has spread.

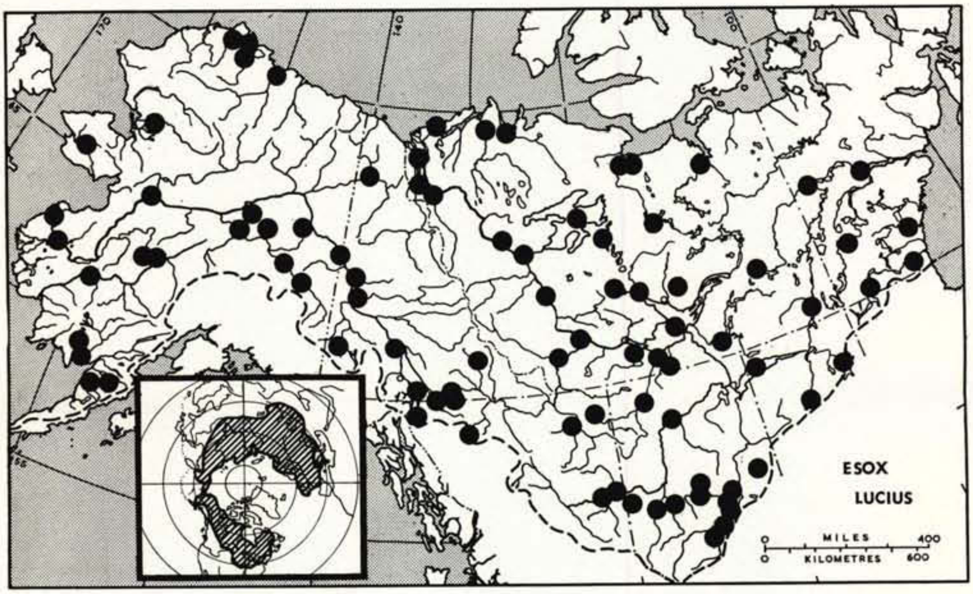
Biology

Arctic records of this species are all from fresh water, but it ventures at least into brackish waters farther south. It lives mostly in lakes or streams, with some populations as far inland as Great Bear Lake on the Mackenzie system. Spawning is reported to occur in April or May near Vladivostock; in Copper River, Alaska, specimens were ripe on June 8. There is little information on the species in our area. The following data are mostly from unpublished studies by Drs D. W. Narver, Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C., and R. L. Wallace, University of Idaho, Moscow, Idaho. In Black Lake (Chignik River system, Alaska Peninsula) spawning occurs in late June in littoral areas over bottoms that are largely covered with organic debris. Some stream spawning may occur. The eggs are adhesive and hatch in about 18 days at 10 C (50 F) (Hamada, 1961). The first larvae taken in Black Lake were collected in plankton townets about July 30. By September the young-of-the-year have reached an average length of about 30 mm, and 1- and 2-year-old fish average about 60 and 80 mm. In Black Lake very few pond smelt live longer than 3 years. The adults are pelagic and feed mainly on zooplankton. Jordan and Evermann (1896) write, concerning pond smelt, "Alaska and Kamchatka, spawning in freshwater ponds, excessively abundant about St. Michaels. A sweet little fish, excellent as food." Pond smelt are of no commercial importance in our area. They are certainly edible and may be used as food in some regions. In Black Lake they have no known predators. In the large Alaskan salmon lakes pond smelt are often abundant, and since they are pelagic and feed on similar organisms as do juvenile sockeye salmon they may have some effect on salmon production in these lakes.

THE PIKES — Family ESOCIDAE

The pike is a long voracious fish described by Izaak Walton as the "fresh-water wolf." All pikes have a flattened snout and large tooth-filled mouth, with dorsal fin far back on a slender body. All are fish-eaters. In the north they serve as human or dog food. Some grow very large, and are a challenge to anglers. All members of the family spawn in spring, scattering eggs in shallow weed beds or grassy flooded land. There is only one genus with five species, confined to fresh waters of Eurasia and America. Only *Esox lucius* enters our area.




ESOX
LUCIUS
MILES
400
KILOMETRES
600

NORTHERN PIKE

Esox lucius Linnaeus

Esox is the name of a large fish mentioned by Pliny and *lucius* is the Latin name of the pike. The French common name for this species is *grand brochet.*

Distinguishing Characters

The long, flattened snout, large mouth with many teeth, and the backward placement of the dorsal fin.

Description

Body long and narrow; head long, about one-third standard length; snout long and flattened. Lower jaw projecting; large canine teeth on the dentary; numerous well-developed teeth on premaxilla, head and shaft of vomer, palatines, tongue, and basibranchials; no teeth on the maxilla. Branchiostegal rays 13–16 + 14–16; gill rakers reduced to flat, denticulated plates, 15–19 on first arch. Dorsal fin originates slightly in advance of anal fin origin; 17–22 total dorsal rays in our area (17–25 elsewhere); 14–18 total anal rays in our area (14–21 elsewhere); 14–16 pectoral rays in our area (14–17 elsewhere); and 10 or 11 pelvic rays. Scales small, cycloid, and embedded; lateral line with 55–65 pored scales, and 105–140 scale rows (105–148 elsewhere). Vertebrae 57–64 (57–65 elsewhere). No pyloric caeca.

Size: Length to over 122 cm (4 ft), and maximum weight in excess of 18 kg (40 lb). A 49-lb pike was taken from Quebec in 1890.

Sexual dimorphism: There are no obvious external differences between the sexes.

Colour: In adults the back and sides are dark green to dark brown, the sides with irregular light yellow spots roughly arranged in vertical rows; the underside is usually a yellow–white. The dorsal, anal, and caudal fins have large dark blotches. In young specimens (less than 25 cm or 10 inches long) there are 10–15 pale vertical bars on the sides, and the spotting on dorsal, anal, and caudal fins is indistinct. Occasionally, a completely silver pike is taken.

Distribution

Circumpolar in fresh water. In arctic drainages, from Scandinavia to Labrador; south in Europe to Italy; south in eastern Asia to Korf Bay and the Penzhina River, and in Alaska to Bristol Bay drainages. Absent from Pacific drainages except in headwaters of the Alsek River (Pine Lake), and the Taku River (Taysen Lake). In most Bering Sea and Arctic Ocean drainages of mainland Canada and Alaska, except not reported from northern Keewatin; not found on the arctic islands. Absent from Peace River drainages upstream of Peace River Canyon. South to eastern Nebraska, Missouri, and the Hudson River.

Taxonomic Notes

Linnaeus referred to the European pike in 1758 as *Esox lucius. Esox estor* was named from Lake Erie by LeSueur in 1818, but these and several other American names are synonyms for *Esox lucius.*

There are at least two morphological forms of pike in our area. Fish found in the Yukon system and other Bering Sea drainages, as well as those along the arctic slope of Alaska, are characterized by high vertebral counts (60–64, with the means usually near 62); pike in the Mackenzie system and the river systems to the east and south are characterized by low vertebral counts (57–62 with the means usually near 59 or 60). Morrow (1964) has demonstrated similar mean differences in dorsal, anal, pectoral, and pelvic fin rays between Alaskan and northeastern American *E. lucius.* These differences are probably attributable to isolation in widely separated glacial refuges. However, recognition of more than one North American subspecies does not seem justified in the present state of knowledge.

Postglacial Dispersal

Pike probably entered the upper Mackenzie system by spreading northward from a refuge in the Mississippi basin. They have reached the lower Mackenzie but have not yet occupied all of the northeastern Barren Grounds. Alaskan populations, with higher vertebral counts, probably originated in an arctic refuge in the Bering region. Pike have probably entered headwaters of the Alsek and Taku systems on the Pacific slope through headwater capture. They failed to ascend the Peace River above the Peace Canyon and will probably not be found upstream of the Portage Mountain Dam at Hudson Hope.

Biology

The northern pike is a fish of shallow lakes and bays, and quiet rivers. Rawson (1951) noted that 90% of the pike taken by gillnetting in Great Slave Lake were within one-quarter mile of shore. Pike are voracious feeders, eating mainly fishes of all available species (including their own kind), but also insects, leeches, small birds, and small mammals. Johnson (1966) has found through experiment that "a mean pike will consume annually between three and four times its mean annual weight"; in a small pike 70% of its total food intake goes into growth and only 30% into body maintenance, which is an unusually efficient use of food. In large pike, however, much of the food intake goes to body maintenance. In southern areas young pike reach 20–30 cm (8–12 inches) by their first autumn, but in the Mackenzie system 1-year-old pike do not exceed 10 cm (4 inches) in length. In Great Bear Lake, males mature at 5 years of age, females at about 6 years (Miller and Kennedy, 1948). In Cree Lake, northern Saskatchewan, it takes nearly 25 years for a pike to reach 25 lb (Rawson, 1959). An early Canadian reference to pike is by Samuel Hearne, who wrote of Lake Athabasca in 1772: "Pike are also of an incredible size in this extensive water; here they are seldom molested, and have multitudes of smaller fish to prey upon. If I say that I have seen some of these fish that were upwards of forty pounds weight, I am sure I do not exceed the truth." Hearne probably did not exceed the truth, but there seems to be a temptation to do so in recounting tales of this species. Gesner reported a pike taken in Sweden in the fifteenth century with a ring about its neck, on which an inscription in Greek declared that the fish had been put in the pond by Frederick the Second 267 years previously. Its skeleton, 17 ft long, was at one time preserved in the Cathedral of Manheim, but doubters declared that it had apparently been manufactured out of the bones of smaller fishes. More credibly, Berg (1948–49) writes that pike weights up to 65 kg (131 lb) are reported from the lower Dnieper River; he also records an eye-witness account of a pike taken in 1930 from Lake Ilmen, south of Leningrad, that weighed 34 kg (69 lb).

The pike spawns in the spring shortly after ice breakup, usually in weedy flooded areas. Males were ripe on June 4 in Kotcho Lake, northeastern British Columbia. Each female may lay several tens of thousands of adhesive eggs, which are scattered over the bottom or on submerged vegetation. In southern areas they hatch in 12–14 days. There is evidently no parental care.

Man's attitude to the northern pike shows surprising geographic variation. In some areas pike are disdained by anglers as slimy "snakes"; in others they are highly prized and intensively pursued for the sport they afford. In Canada's Prairie Provinces pike fishing greatly exceeds any other sport fishery, and pike are the goal of many airborne angling trips into lakes of the Precambrian Shield.

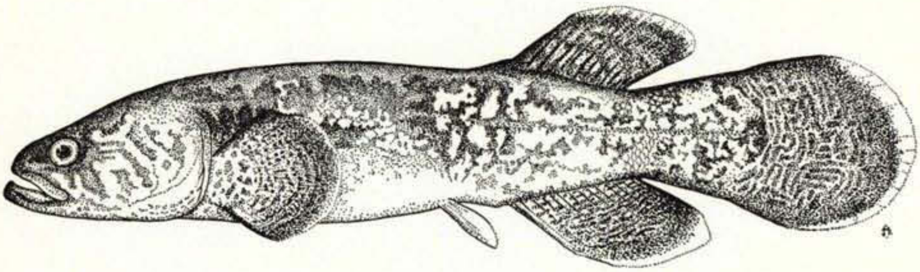
The flesh of pike from cool water is firm and has good flavour. Taken in gillnets, pike are used as human and dog food throughout the north, and are exported to the United States in commercial quantities either fresh or frozen. On this continent, however, pike does not enjoy a particularly high reputation as food. Europeans are more appreciative of the culinary possibilities of pike; recently Canadian pike, dressed but with heads intact, are finding an increasing market in France and in Germany. Large pike are delicious baked; Izaak Walton (1653) gives a mouth-watering recipe for stuffed pike, including sweet marjoram, pickled oysters, mace, claret wine, and anchovies. The mucus that covers the pike has sometimes a rather strong odour that may be removed by skinning the fish before cooking it.

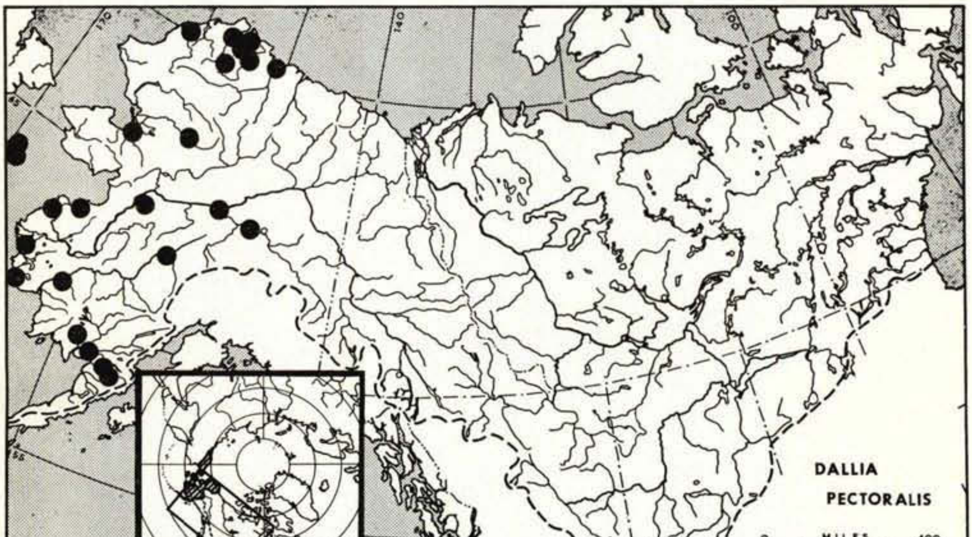
In early England different names were used for different growth stages of this species, and these names have been variously misapplied to New World fish. "Jack" originally referred only to the young or fry of the pike, but in North America "jack" or "jackfish" commonly means a northern pike of any size. In 1587 "pickerell" meant a half-grown pike, but now it is erroneously used in some places for northern pike, in others for walleye; the name "pickerel" should now be reserved for smaller members of the genus *Esox* (the redfin pickerel, the grass pickerel, and the chain pickerel). The word "luce" formerly referred to a large pike.

The significance of pike as a host for the tapeworm *Triaenophorus crassus* is discussed under the "Biology" section of the lake whitefish *"Coregonus clupeaformis"* complex.

THE BLACKFISH — Family DALLIIDAE

The blackfish is a unique little blunt-headed fish adapted to the fresh waters of the tundra. The family is related to the pikes (family Esocidae) and also to the mudminnows (family Umbridae) with which it is lumped by some authors, but is distinguished by the absence of several bones in the fin supports. There is only one species of *Dallia,* found only in Siberia and Alaska. In the family Umbridae, the central mudminnow *Umbra limi* (Kirtland) occurs in the Nelson River drainage in Manitoba and perhaps even closer to our area; it presents somewhat the same appearance as the blackfish, but has fewer pectoral and anal fin rays (14 and 8 respectively) and larger scales (about 35).




DALLIA
PECTORALIS
0 MILES 400
0 KILOMETRES 600

BLACKFISH

Dallia pectoralis Bean

Dallia is named for Dr W. H. Dall, its discoverer, and *pectoralis* alludes to the broad pectoral fins. The French common name for this species is *dallia*.

Distinguishing Characters

The backward placement of the dorsal fin, the three pelvic fin rays, and the rounded pectoral and caudal fins.

Description

Body slender, round in cross-section; head short, less than one-quarter total body length; eye small, about 5 into head; snout short and somewhat pointed. Lower jaw projecting; well-developed teeth on the dentary, premaxillary, head of vomer, and palatines; no teeth on the maxillary, tongue, or basibranchials. Branchiostegals 7–8 + 7–8; gill rakers short, 1–2 + 8–10. Dorsal fin originates directly above origin of anal fin; 10–14 total dorsal rays; 12–16 anal rays; 32–36 pectoral rays; 0–3 (usually 3) pelvic rays. Scales small, cycloid, and embedded; lateral line complete but made up of very small pores; 76–100 scales along lateral line. Vertebrae 40–42. No pyloric caeca.

Size: Wynne-Edwards (1952) records a maximum length of 200 mm (about 8 inches). The largest we have seen was a male 165 mm in length (about 6.5 inches) and about 50 g (1.5 oz) in weight.

Sexual dimorphism: In mature males the dorsal and anal fins almost reach the base of the caudal fin, and the pelvic fins extend well beyond the origin of the anal fin; in females the dorsal and anal fins are much shorter than in males, and the pelvic fins do not extend to the origin of the anal fin.

Colour: Adults are dark brown above, with four to six dark bars on sides; underside is pale with dark brown speckling. The fins are speckled with dark brown, and the dorsal, anal, and caudal fins are rimmed with white (reddish in males at spawning time). This white rim is more pronounced in mature males than in females or juveniles. Juveniles have essentially the same colour pattern, but the brown colour is lighter. Young blackfish, less than 1 inch long, have three distinct dark spots at the base of the caudal fin. Adult individuals completely lacking pigmentation on some parts of the body are occasionally collected in the Bethel area (lower Kuskokwim River).

Distribution

The Chukotsk Peninsula, Siberia, and lowland areas in Alaska, from the central Alaska Peninsula (Chignik area) north along the arctic coast to the Colville River, and on St. Lawrence, St. Matthew, and Nunivak islands in the Bering Sea; inland in the Yukon system to the Fairbanks area. The population on St. Paul Island (Pribiloff Islands) is apparently an introduction, as is the population in Hood Lake near Anchorage.

Taxonomic Notes

T. H. Bean described *Dallia pectoralis* from St. Michaels, Alaska, in 1879. The only synonym is *Umbra delicatissima* Smitt. Morphologically the blackfish appears to be relatively stable with little geographic variation.

Postglacial Dispersal

The range of *Dallia* is almost restricted to the Bering glacial refuge. In addition the presence of *Dallia* on St. Lawrence and St. Matthew islands (both remnants of the Bering land bridge) indicates that it was present in the Bering refuge during glaciation. Apparently *Dallia* has not significantly expanded its range postglacially.

Biology

The blackfish is typically an inhabitant of weed-choked lowland swamps and ponds. However, it also occurs in streams, rivers, and even large lakes if there is an abundance of aquatic vegetation. *Dallia* is most common in tundra regions, but is also found in forested areas when suitable habitat is available.

The blackfish is rather sluggish and spends much of its time hovering almost motionless among the weeds. It feeds by slowly sculling (with the pectoral fins) to within a few inches of its prey and then making a sudden dart forward. The food consists mainly of insect larvae, crustaceans, ostracods, and various types of snails. Young blackfish feed on similar but smaller organisms. Growth is rapid in the first summer; in the Bristol Bay region the young-of-the-year average 20 mm in length by September (N. Aspinwall, personal communication). Some females reach maturity in their 2nd year, but most spawn for the first time in their 3rd year at a length of about 50 mm. The oldest age recorded for blackfish is 8 years (N. Aspinwall, personal communication).

Virtually nothing is known about the spawning of blackfish. Aspinwall estimates that in the Bristol Bay area spawning occurs mainly in July, apparently in shallow water amid dense vegetation. The eggs are about 2 mm in diameter, adhesive, and demersal. They are probably attached to plants or material on the bottom, but there are no recorded observations on naturally spawned *Dallia* eggs. Nothing is known about the spawning behaviour. Female blackfish normally contain about 100 ripe eggs, but a large female may contain as many as 300. At about 54 F (12 C) under artificial conditions hatching takes about 9 days.

The supposed ability of the blackfish to withstand freezing is legendary in Alaska. Turner (1886) says "The vitality of these fish is astonishing. They will remain in those grass baskets for weeks, and when brought into the house and thawed they will be as lively as ever. The pieces which are thrown to the ravenous dogs are eagerly swallowed; the animal heat of the dog's stomach thaws out the fish, whereupon its movements soon cause the dog to vomit it up alive. This I have *seen*, but have heard some even more wonderful stories of this fish." Various scientists have investigated the ability of *Dallia* to withstand freezing, and all have concluded that although the blackfish is resistant to low temperatures it can not withstand freezing of the body tissues.

Blackfish are unimportant commercially, but in the past have been a significant food fish especially in the Kuskokwim and Yukon delta regions. Turner (1886) indicates that the Alaskan natives trapped blackfish for dog food and for their own use. "From May to December, tons and tons of these fish are daily removed. They form the principal food of the natives living between the Yukon Delta and the Kuskokwim River. . . ." Such an extensive fishery for blackfish is no longer in existence although they are still used to some extent for human food. A local Alaskan name for this species is "devilfish."

Dallia makes an attractive aquarium fish and does well at normal room temperatures. In captivity it will readily take earthworms and other live food.

THE MINNOWS — Family CYPRINIDAE

One-fourth of the world's total of known fish species belong to the order Cypriniformes (or Ostariophysi). Included are the suckers (family Catostomidae), minnows (Cyprinidae), loaches, characins, gymnotid eels, and over 25 families of catfishes. These diverse fishes, which together dominate the fresh waters of all continents except Australia, have in common a Weberian apparatus. This is a complex modification of the first four or five vertebrae, with a chain of small bones on either side connecting the front end of the double-chambered gasbladder to the inner ear in the skull. Its purpose may be sound or pressure detection, or some other function as yet unknown.

The minnows, family Cyprinidae, are usually small fishes with toothless jaws but without the wide fleshy lips of suckers, cycloid scales, a single soft dorsal fin, and no adipose fin. Lacking teeth in the mouth, they have developed strong teeth in the throat, carried on the inside of the fifth gill arch. These pharyngeal teeth may be hooked for tearing, or blunt for grinding, and are in 1–3 rows on each side. They bite against a horny pad at the base of the skull. Pharyngeal tooth counts are given in a formula from left to right. Thus the formula 2,5–4,2 means that the pharyngeal bone on the left side of the throat has 2 teeth in the outer row and 5 in the inner, and the right bone has 4 inner teeth and 2 outer.

Minnows in our area are mostly small and of little commercial note. They spawn in spring or summer. The sexes often show distinctive colouration at breeding time, and males may develop horny protuberances on the body or fins. In different species, spawning may be in still or in running water; eggs may be broadcast and deserted, or may be guarded by the male.

The Cyprinidae constitute the largest family of fishes in the world, with about 275 genera and 1500 species. They probably originated in Asia, where they are most abundant, and spread from there into Africa and also, via the Bering region, into North America. No cyprinids have reached South America. In the Old World they occur in great variety, including forms with long-based dorsal fins and some with stout spines before the dorsal and anal fins. (The carp and goldfish are examples that have been introduced by man into North America.) In contrast, American minnows are relatively uniform, the majority belonging in the one subfamily Leuciscinae. About 200 American species are recognized; because they form a rather closely knit group, their classification into genera is controversial. Thirteen species reach northward into our area, where most are confined to the Mackenzie system.

KEY TO THE SPECIES

1(10) Barbel present near the corner of the mouth (Fig. 20, 22, 23) (sometimes merely a small hairlike projection in young fish) 2

2(3) No groove between upper lip and tip of snout (Fig. 20); snout long and overhanging .... Longnose dace, *Rhinichthys cataractae* (Valenciennes) .... (p. 247)

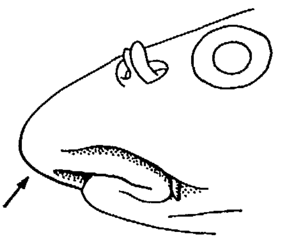


Fig. 20. Head of *Rhinichthys cataractae,* showing upper lip fused to snout.

3(2) A distinct groove between upper lip and tip of snout 4

4(5) Upper jaw extends to, or beyond, front margin of eye; length of barbel equal to or greater than half the eye diameter; pectoral fins long and sickle-shaped, the outer ray longer than the third .... Flathead chub, *Platygobio gracilis* (Richardson) (p. 237)

5(4) Upper jaw not reaching front margin of eye; barbel length less than half the eye diameter; pectoral fins more rounded, the outer ray shorter than the third 6

6(7) Pelvic axillary process present (Fig. 21); front of dorsal fin base lies opposite or ahead of front of pelvic fin base; tail deeply notched, its middle rays less than or about equal to half the longest rays .... Peamouth, *Mylocheilus caurinus* (Richardson) .... (p. 233)

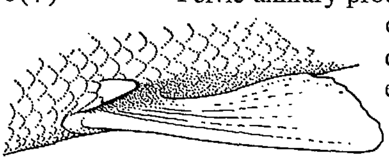


Fig. 21. Pelvic axillary process, *Mylocheilus caurinus.*

7(6) Pelvic axillary process absent; front of dorsal fin base either opposite or behind front of pelvic fin base; tail less deeply notched, middle rays distinctly more than half length of longest rays 8

8(9) Barbel minute, leaflike, and wholly concealed in groove when mouth is closed (Fig. 22); length of dorsal fin base equal to or less than least caudal peduncle depth .... Northern pearl dace, *Semotilus margarita nachtriebi* (Cox) .... (p. 229)

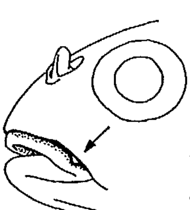


Fig. 22. Head of *Semotilus margarita,* showing small leaflike barbel.

9(8) Barbel well developed, visible at the posterior corner of mouth when mouth closed (Fig. 23); length of dorsal fin base greater than least caudal peduncle depth .... Lake chub, *Couesius plumbeus* (Agassiz) (p. 243)

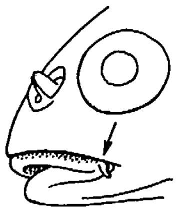


Fig. 23. Head of *Couesius plumbeus,* showing larger barbel.

10(1) No barbel on the upper jaw 11

11(20) Lateral line scales small (more than 55 in lateral line) 12

12(13) Snout long (about $1\frac{1}{2}$ or more times horizontal eye diameter) and pointed; mouth large; young with a black spot at base of tail .... Northern squawfish, *Ptychocheilus oregonensis* (Richardson) .... (p. 225)

13(12) Snout short (usually about equal to horizontal eye diameter) and blunt; mouth smaller; young without black spot at base of tail .. 14

14(15) Anal fin long, 10–22 anal rays (usually 13 or more) .... Redside shiner, *Richardsonius balteatus* (Richardson) (p. 221)

15(14) Anal fin short, 7–8 anal rays (occasionally 9) 16

16(19) Lateral line incomplete; lining of body cavity jet black 17

17(18) Upper jaw extends to front margin of eye; a single dark lateral stripe .... Finescale dace, *Pfrille neogaea* (Cope) (p. 251)

18(17) Upper jaw does not extend to front margin of eye; two dark lateral stripes .... Northern redbelly dace, *Chrosomus eos* Cope (p. 255)

19(16) Lateral line complete; lining of body cavity light or slightly speckled .... Northern pearl dace, *Semotilus margarita nachtriebi* (Cox) .... (p. 229)

20(11) Lateral line scales large (fewer than 52 in lateral line) 21

21(28) Anal fin with 7 or 8 rays; front of dorsal fin base either opposite or ahead of pelvic fin base 22

22(23) A large, conspicuous and well-defined black spot at base of caudal fin .... Spottail shiner, *Notropis hudsonius* (Clinton) (p. 263)

23(22) No conspicuous black spot at base of caudal fin 24

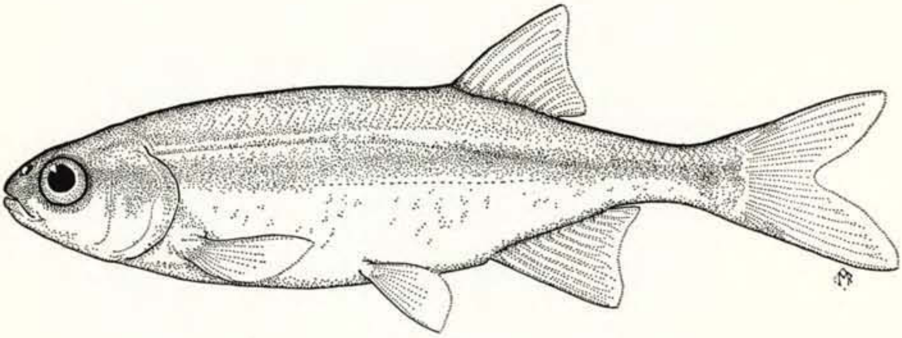
24(25) Lateral line usually incomplete; usually 40 or more scale rows along side; front of dorsal fin base lies directly opposite front of pelvic fin base ....
.... Fathead minnow, *Pimephales promelas* Rafinesque (p. 271)

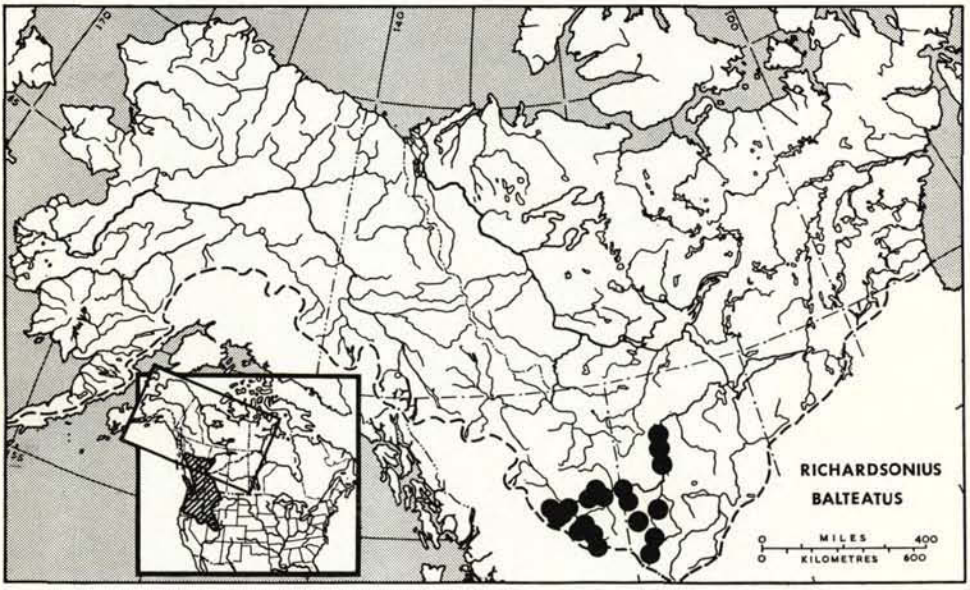
25(24) Lateral line complete; usually 39 or fewer scales in lateral line; front of dorsal fin base either opposite or ahead of pelvic fin base 26

26(27) Lining of body cavity black, intestine greatly elongated, much coiled on right side; front of dorsal fin base ahead of pelvic fin base ....
.... Brassy minnow, *Hybognathus hankinsoni* Hubbs (p. 267)

27(26) Lining of body cavity silvery, intestine not greatly elongated (less than twice standard length); front of dorsal fin base directly above front of pelvic fin base .... River shiner, *Notropis blennius* (Girard)
This species not recorded from our area, but known from the Saskatchewan River system.

28(21) Anal fin with 10–13 rays (rarely 9); front of dorsal fin base well behind front of pelvic fin base ....
.... Emerald shiner, *Notropis atherinoides* Rafinesque (p. 259)




RICHARDSONIUS
BALTEATUS
MILES
400
KILOMETRES
600

REDSIDE SHINER

Richardsonius balteatus (Richardson)

Richardsonius is named after Sir John Richardson, surgeon and naturalist on the early Franklin expeditions, and *balteatus* means *girdled*. The French common name for this species is *méné rose*.

Distinguishing Characters

The long anal fin base and backward placement of the dorsal fin.

Description

Body deep and strongly compressed; head moderate, about one-quarter length; eye large, about equal to snout. Mouth small, oblique, extends back almost to the front margin of the eye, lower lip protruding very slightly beyond snout and upper lip when mouth closed; no barbel; pharyngeal teeth usually 2,5–4,2. Branchiostegals 3 + 3; gill rakers short, a total of 6–9 on the first arch. Dorsal fin originates well behind the origin of the pelvic fins, centre of dorsal fin base lying behind origin of anal fin; 8–12 dorsal rays, usually 9 or 10; 10–22 major anal rays (usually 12–18 in our area); 14–16 pectoral rays; and 9 pelvic rays. Pelvic axillary process present. Scales small, cycloid, 55–67 pored scales in the complete lateral line; lateral line strongly decurved, running parallel to the ventral surface. Vertebrae 38–43 (usually 40–42 in our area), including the 4 elements of the Weberian region. Intestine short; peritoneum lightly speckled.

Size: To 180 mm (7 inches), but usually less than 127 mm (5 inches).

Sexual dimorphism: Males, but not females, develop numerous small tubercles on the head and the upper surfaces of pectoral and pelvic fins. The pectoral tips reach nearly to the pelvic fin bases in males but not in females. Breeding males are lean, dark, and vividly coloured, whereas females tend to be fat and paler.

Colour: Back dark olive or brownish, belly silvery. A dark lateral band from snout to base of tail, with a light streak from above the eye fading out below the dorsal fin. A red wash of varying intensity behind the gill cover, at base of pectorals, and along the light streak. The males are brilliant at spawning time, with metallic gold on the head, fins, and sides, alternating with vivid crimson.

Distribution

Pacific slope drainages from the Nass River south to the Columbia River basin and coastal drainages of Oregon. In the Malheur basin in Oregon, and Salt Lake drainages in Utah. Introduced into the Colorado River. In the Mackenzie River system, so far confined to the upper Peace River system in British Columbia, and downstream in Alberta almost to Fort Vermilion.

Taxonomic Notes

The redside shiner was first described from the Columbia River by Sir John Richardson in 1836 as *Cyprinus (Abramis) balteatus*. When Girard later (1856b) proposed a distinct New World genus he named it *Richardsonius* after Richardson, which explains why the scientific name both commemorates the man and attributes the specific name to him. The Old World genera *Leuciscus* and *Abramis* have at times been used for this minnow. Because of its extraordinary variability, many different species were named that are now thought to represent this one, including *lateralis, gilli, siuslawi, thermophilus, montanus,* and *hydrophlox*. Currently only one other species is recognized in the genus, *Richardsonius egregius,* occupying the Lahontan basin of Nevada.

Anal fin ray count varies enormously in this species. Although some variability is due to direct modification of the developing young by temperature, a genetic tendency towards higher ray counts in the northern end of the range has been demonstrated by experimental rearing (Lindsey, 1953, and unpublished data). Until the sources of variability are better understood, it seems unwise to recognize different subspecies.

Postglacial Dispersal

The range of the redside shiner includes only one glacial refuge, the Pacific. The populations in our area were derived through postglacial dispersal northward from the Columbia system into the Fraser River, and from the Fraser system east across the Continental Divide into the upper Mackenzie system.

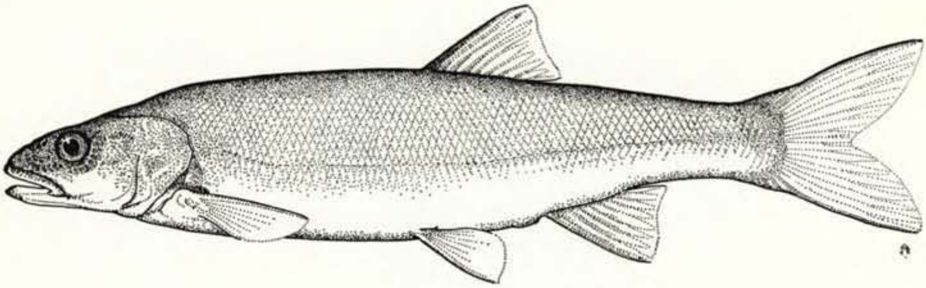
Biology

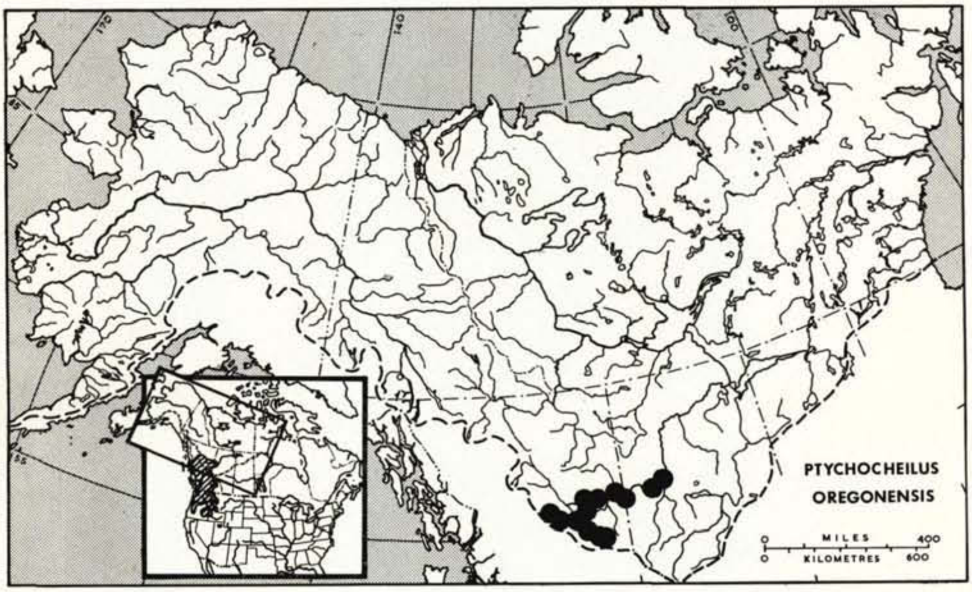
Redside shiners may be abundant in lakes, ponds, or slow rivers. Both young and adults school. They have regular daily and seasonal patterns of movement, swimming from the shallows out over deep water on calm nights, and moving down into deeper water during winter (Crossman, 1959). Food includes aquatic and terrestrial insects, molluscs, plankton, and sometimes small fish. Studies on a small lake in central British Columbia (Lindsey and Northcote, 1963) showed the shiner population to have surprisingly low rates of recruitment, growth, and death, with first spawning in the 4th year of life, and some fish living 6 or 7 years.

Spawning in central British Columbia may extend from early May until late July in different areas. Eggs are usually deposited over the gravel bottom of inlet streams, but in some places eggs are shed amongst submerged plants near the lakeshore. The eggs are small, yellow, and adhesive when laid. There is no nest building or guarding by the parents; eggs adhere singly or in small clusters wherever they fall. Fry emerging in inlet streams move downstream during periods of darkness; once in the lake they feed at first very close to shore, gradually occupying deeper water as they grow.

Redside shiners have been deliberately introduced into some British Columbia lakes with the expectation that they would serve as food for rainbow trout. Although large trout do feed extensively on shiners under some circumstances, the overall effect of shiners on rainbow trout production is likely to be detrimental, for shiners may severely compete with, and vastly outnumber, young trout. Large shiners can also eat small trout. Costly programs of shiner eradication by poisoning have been resorted to in other British Columbia lakes. Neither the effect of introducing a new fish species, nor of eradicating species by poison, can accurately be foreseen, for each lake is a different and complex microcosm. In general, most introductions of redside shiners or other "forage fish" have failed to achieve their objectives. By the same token, removal of all nonsport fish often has not produced a good sport fishery.

Redside shiners have evidently crossed the Continental Divide from west to east only recently (geologically speaking) and are probably still extending their range into Alberta. They occur throughout the upper Peace River system in British Columbia; in Alberta they have not yet been taken in the mainstem Peace River, but are abundant in the upper Wapiti River. Perhaps redside shiners have crossed the Continental Divide at more than one point.




PTYCHOCHEILUS
OREGONENSIS
0 MILES 400
0 KILOMETRES 600

NORTHERN SQUAWFISH

Ptychocheilus oregonensis (Richardson)

Ptychocheilus means *folded lip* and *oregonensis* means *of Oregon.* The French common name for this species is *sauvagesse du nord.*

Distinguishing Characters

The elongate snout, absence of barbels, and the large mouth extending back beyond the front margin of the eye.

Description

Body elongate, slightly compressed; head long, tapered, more than one-quarter standard length; eye moderate, about one-half snout length. Mouth large, slightly oblique, upper jaw extends past front margin of the eye except in small fish; front of upper lip projecting beyond snout and lower lip; no barbel. Pharyngeal teeth usually 2,5–4,2, conical, slightly curved at tips. Branchiostegals 3 + 3; gill rakers short, best developed near the angle of the arch, a total of 8–11. Dorsal fin originates above, or slightly behind, the origin of the pelvic fins; 8–10 major dorsal rays; 7–10 major anal rays; 15–18 (usually 16) pectoral rays; and 9 pelvic rays. Pelvic axillary process present or absent. Base of dorsal fin about 1.3 times depth of caudal peduncle. Scales small, cycloid, 65–76 pored scales in the complete lateral line. Vertebrae 40–43 (including the 4 elements of the Weberian region). Intestine short; peritoneum lightly speckled below and dark above.

Size: Up to 63 cm (25 inches) in length. A 13-kg (29-lb) northern squawfish was taken in Shuswap Lake, B.C., but its length was not recorded.

Sexual dimorphism: Breeding males, but not females, develop small tubercles on the top of the head, back, pectoral, pelvic, and caudal fins; the pelvic fins when depressed usually reach the vent in males but not in females.

Colour: Adults are dark green to brown on the back and silver or pale yellow below. All fins are immaculate. An indistinct dark stripe is usually present along the posterior midlateral line. At spawning time males develop bright orange pectoral, pelvic, and anal fins, and a distinct white line develops below the lateral line. The young are similar to the adults in colour except that the dusky midlateral stripe is more pronounced and there is a distinct black spot at the base of the caudal fin.

Distribution

On the Pacific slope from the Nass River south to the Columbia River systems, and in Malheur Lake of Oregon. East of the Continental Divide, only in the upper Peace River system in British Columbia and as far east as Peace River townsite in Alberta.

Postglacial Dispersal

The range of the northern squawfish includes only one glacial refuge, the Pacific. The populations in our area were derived by postglacial dispersal from the Columbia system north to the Fraser River, and from the Fraser River east across the Continental Divide to the upper Peace River (Mackenzie system).

Taxonomic Notes

The northern squawfish was originally described from the Columbia River by Richardson in 1836 as *Cyprinus (Leuciscus) oregonensis*. The specific names *major* and *gracilis* have also been applied. Three geographically isolated forms that are currently considered to be distinct species are *Ptychocheilus umpquae* in Oregon coastal drainages, *P. grandis* in the Sacramento River area, and *P. lucius* in the Colorado River.

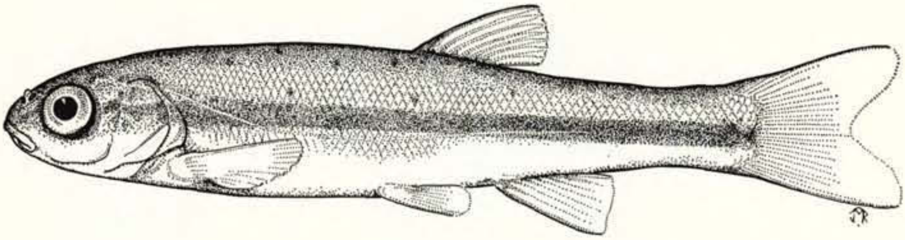
Biology

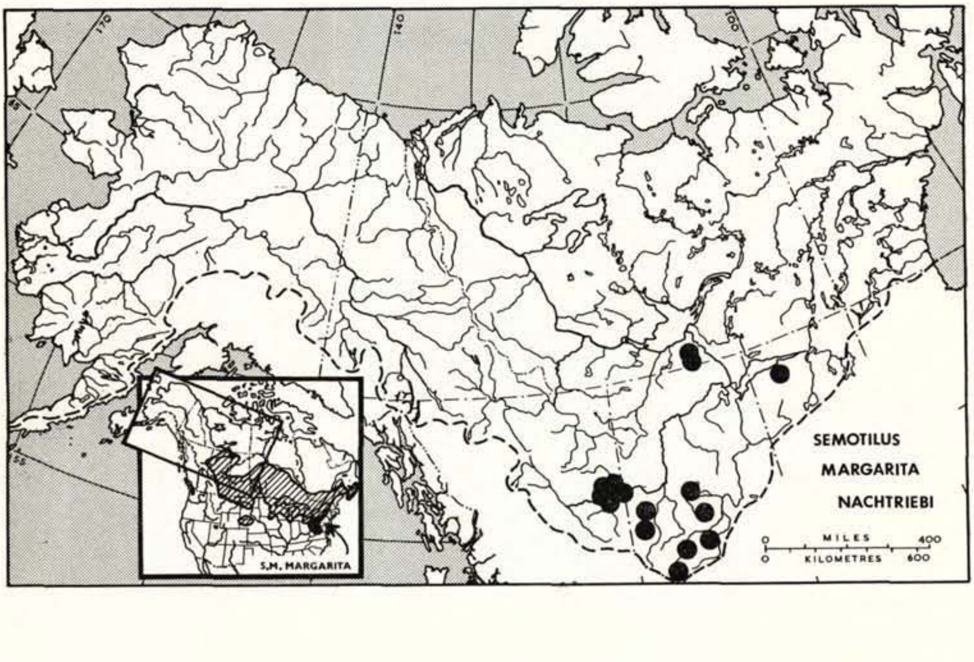
Northern squawfish are primarily lake fish, and occupy only slow or moderate streams and rivers. They are usually found close to shore during summer months, but apparently move into deeper water in winter. They are usually taken close to the bottom, occasionally in quite deep water (to depths of 36 m (78 ft) in Washington). In British Columbia the young and juveniles feed on terrestrial insects, insect larvae, plankton, and molluscs. Even squawfish 87 mm (3.5 inches) long may eat fish, and fish form the principal diet of adults. Squawfish are catholic feeders; even large individuals sometimes feed heavily on surface insects, and one has been found that had eaten a toad. Although squawfish, like all cyprinids, lack jaw teeth, they have large sharp hooked pharyngeal teeth in the gullet, painfully evident to the angler unwise enough to push his finger down the throat of a large specimen. Squawfish have evolved west of the Continental Divide, in an area lacking pike (*Esox lucius*). Here the squawfish, with its large mouth, sharp throat teeth and predatory habits, follows fish-eating habits somewhat comparable with those of the northern pike elsewhere. Squawfish have pierced the continental barrier only at the northern end of their range in the Peace River area. Downstream from the Peace River canyon they occupy the river along with pike. Whether they will be able eventually to spread into such areas as Athabasca or Great Slave lakes, and possibly affect the fisheries there, is an interesting question.

In central British Columbia squawfish probably reach sexual maturity in about their 6th year, at a length of roughly 12 inches (probably earlier in males than females). They may live 15 or 20 years. The largest specimen of *Ptychocheilus oregonensis* so far recorded weighed 13 kg (29 lb), but the Colorado form *Ptychocheilus lucius* is reported to reach a weight of 36 kg (80 lb) and a length of 152 cm (5 ft).

Spawning in central British Columbia occurs from late May to early July. Eggs are usually deposited over gravel in inlet or outlet streams close to lakes, or over gravel in shallow standing water. Males remain in large numbers at the spawning site, and females enter the area for brief periods to shed enormous numbers of small greenish adhesive eggs. No nest is constructed.

Northern squawfish are so large as to provide some sport. When hooked they fight by a series of violent tugs. They will rise to a fly, particularly in the evening. Although the slime of the fish is rather smelly, the flesh when properly cooked and seasoned is edible. Referring to its southern relative, Rostlund (1952) writes: "The lower Colorado River tribes used to shoot it with bow and arrow, but the enthusiasm for it seems nowhere to have been any greater than that which Thoreau felt for the fallfish, which he said tasted like brown paper salted." We can add no further data from personal experience.




SEMOTILUS
MARGARITA
NACHTRIEBI
MILES
400
KILOMETRES
600
S.M. MARGARITA

NORTHERN PEARL DACE

Semotilus margarita nachtriebi (Cox)

Semotilus means *spotted dorsal fin*, particularly conspicuous in an eastern species *S. atromaculatus*; *margarita* means *a pearl*; and *nachtriebi* is named after Professor H. F. Nachtrieb, state zoologist of Minnesota. The French common name for this species is *mulet perlé du nord.*

Distinguishing Characters

The small scales, the pale peritoneum, and the weakly developed barbel (often totally absent), not visible when mouth closed except in very large fish.

Description

Body robust, little compressed; head about one-quarter standard length; eye moderate, but less than snout. Mouth oblique, not quite reaching anterior margin of eye; front margin of upper lip projecting slightly ahead of lower lip and snout when mouth closed; barbel small, a flaplike projection arising in the groove above the maxilla (the upper lip) ahead of its posterior tip (Fig. 22), concealed when mouth is shut except in very large individuals, often visible only by magnification, sometimes totally absent; pharyngeal teeth 2,5–4,2 or 2,4–4,2. Dorsal fin originates well behind origin of pelvic fins; 8 major dorsal rays; 8 major anal rays; 15–18 pectoral rays; and 7 or 8 pelvic rays. Peduncle deep, its least depth about equal to dorsal fin base. Scales small, cycloid, slightly embedded in large specimens; lateral line complete except in young (in our area), with 70–79 pored scales (61–79 over whole range of the subspecies). No pelvic axillary process. Vertebrae 38–42 (including the 4 elements of the Weberian region). Intestine moderate, usually one loop; peritoneum pale, or lightly speckled.

Length: Usually 76–102 mm (3 or 4 inches). One specimen from Charlie Lake, Peace River area, is 158 mm (6.25 inches) long.

Sexual dimorphism: Paired fins of males are longer, wider, and rounder than those of females, with the pectorals reaching more than half way back to the pelvic origins in males but not in females. Breeding males have double rows of tubercles on upper surfaces of each of the first 6 or 7 pectoral rays, many tiny tubercles on the head, and short irregular raised ridges on the posterior edges of the scales.

Colour: Dark brownish on back, silvery on belly, scattered dark scales overall. Sides with a dark lateral stripe, sometimes distinct, sometimes faint, particularly towards the anterior, often with a narrower pale stripe immediately above this. Breeding males with a red band low down on the flanks, forward to just behind the eye, and light areas tinged with yellow. Young with distinct brownish lateral band from gill cover to base of tail, where it widens to form a diffuse spot.

Distribution

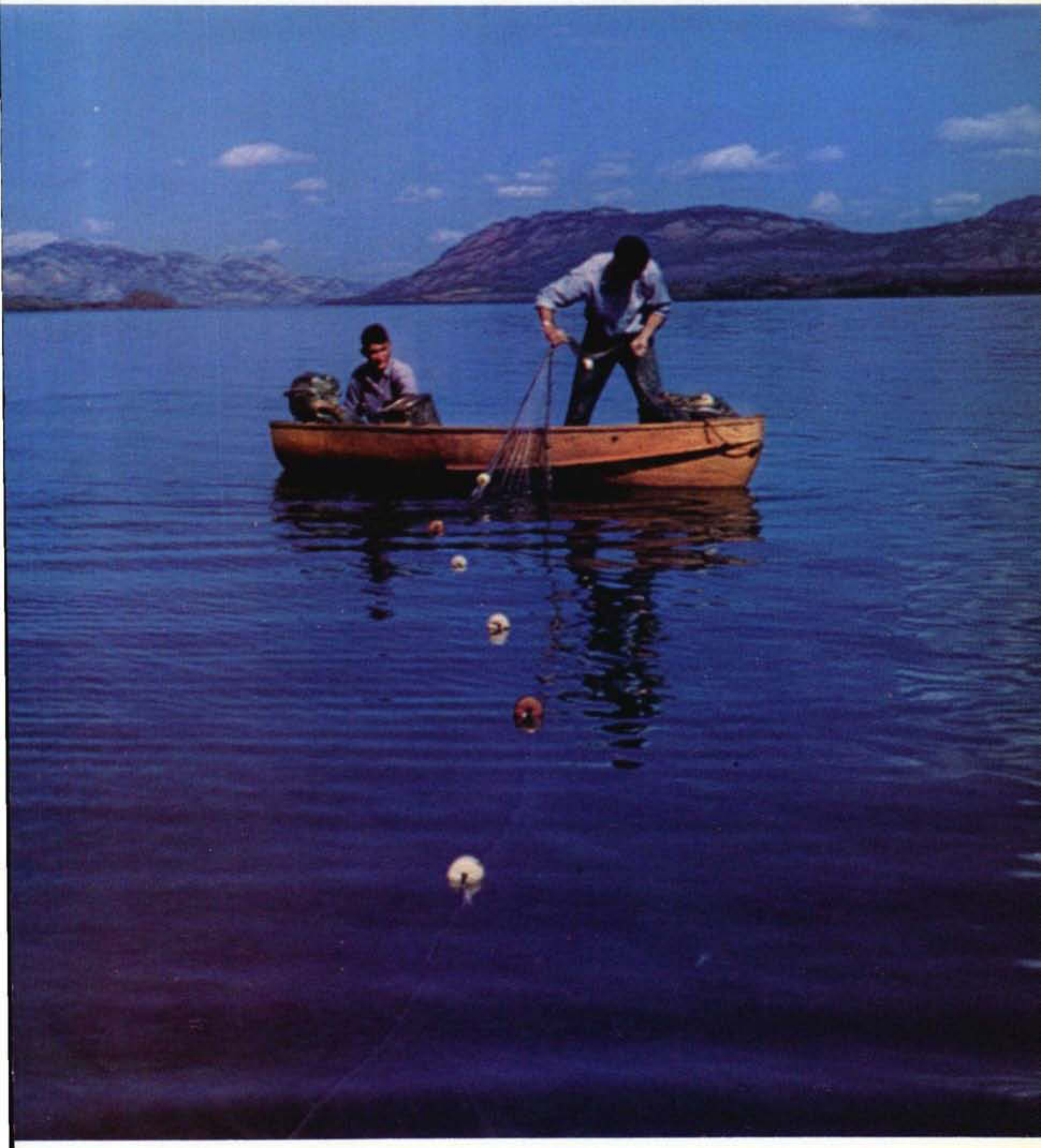
The species ranges from the lower Sass River, N.W.T., east to Nova Scotia, south to Virginia, Wisconsin, and northern Montana, with relict populations in cool springs of Nebraska and South Dakota. The subspecies *nachtriebi* occupies all this area except the Alleghany region and Isle Royale. In our area it has been taken in Athabasca, Peace, and Slave river drainages.

Taxonomic Notes

This subspecies was originally named from Minnesota as *Leuciscus nachtriebi* by Cox in 1896. It was placed in the genus *Margariscus* by Cockerell in 1909, but recently it has been included in the genus *Semotilus.* Bailey and Allum (1962, p. 36) give reasons for placing *Semotilus atromaculatus, S. margarita,* and *S. corporalis* in a common genus. These species "share many characters, including two rows of hooked teeth with the count 5–4 in the main row, a complete lateral line, a terminal mouth of moderate size, scales of moderate size (about 43–78), a modal count of 8 anal rays, a common physiognomy, and, especially, a flaplike barbel located above the maxilla well in advance of its posterior tip." The principal differences, mouth size and nuptial tubercles, relate to differences in breeding behaviour and have been independently evolved several times among American cyprinids and catostomids. These are convincing arguments for lumping these species, formerly in three small genera, to indicate their close relationship.

Two or three subspecies of pearl dace are currently recognized. The wide-ranging form *Semotilus margarita nachtriebi* occurs in our area. *Semotilus m. margarita* has markedly fewer scales; it occupies the Alleghany region, and its range is said to overlap that of *S. m. nachtriebi* in drainages entering lakes Erie, Ontario, and Champlain. Another subspecies *Semotilus margarita koelzi* (Hubbs and Lagler) differs in head, mouth, and lip shape, and is confined to one lake on Isle Royale in Lake Superior. A further subspecies *Semotilus nachtriebi athabascae* (Bajkov) from the Jasper region within our area was named by Bajkov (1927). However, its supposedly distinctive scale count (55–62) is intermediate between those of *S. m. margarita* (49–62) and *S. m. nachtriebi* (61–78) given by Bailey and Allum (1962). The other characters given by Bajkov do not appear to us to be distinctive, nor are

Sampling by gillnet in Lake Laberge, Yukon Territor
Photo: C. C. Lindse



our specimens from Obed Lake, Athabasca drainage, outstanding. Clearly the *margarita* group needs closer study. Since *S. m. margarita* and *S. m. nachtriebi* differ markedly in scale count, and are said to have overlapping ranges, perhaps they will prove to be distinct species (as they were originally designated). If so, our northern form should be called *Semotilus nachtriebi* (Cox). At present, we recognize *margarita* and *nachtriebi* as distinct subspecies, the latter probably including the nominal subspecies *athabascae* and possibly also *koelzi*.

Postglacial Dispersal

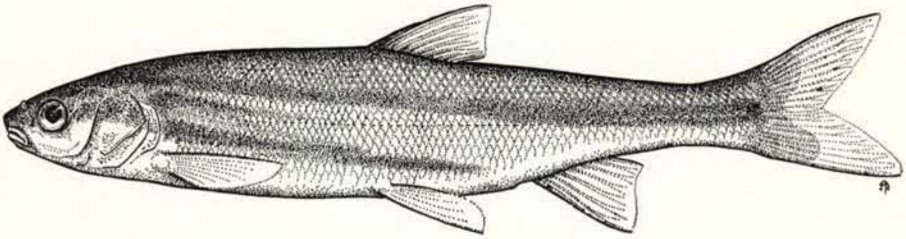
The range of the subspecies of *S. margarita nachtriebi* includes only one glacial refuge, the Mississippi. At present the northern pearl dace is widespread in the upper Mississippi system, but in the Missouri system it is restricted to the upper Missouri (Milk River) and a few relict populations in Nebraska and South Dakota. During Wisconsin glaciation the pearl dace was probably continuously distributed in the upper Mississippi and Missouri systems. Because of the timing and pattern of deglaciation (see "Geological History") the populations in the Missouri system had the first opportunity to disperse northward, and as a result the populations in our area were probably derived from this source.

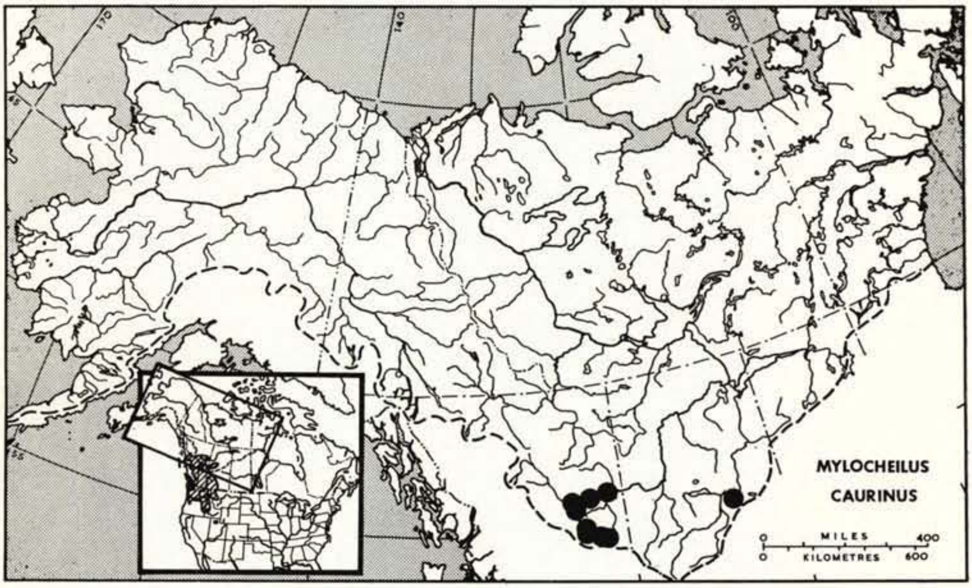
Biology

In our area pearl dace have been taken in lakes and in streams, in clear and muddy water. In the south and east they are reported to favour cool streams or boggy lakes, and to avoid sandy habitats. Stomachs of specimens from our area contain insects (primarily beetles) but also some filamentous algae, some *Chara,* and vegetable debris. Pearl dace in Charlie Lake, Peace River district, have been seen to take flies from the surface after the manner of trout (Cowan, 1939). Elsewhere they are said also to eat animal plankton and various aquatic organisms including small fish.

Spawning has not been observed in our area, but Langlois (1929) described breeding habits of this species in Michigan. Spawning occurred on June 12, in clear water of 63–65 F about 2 ft deep, with sand or gravel bottom, and current varying from strong to almost none. Each adult male defended an area of stream bottom about 8 inches across with no definite outline except as its margin was made apparent by the behaviour of its proprietor. No mound or excavation was observed. The male escorted other invading males away, but drove females into his territory. There the male pressed the posterior of the female against the bottom with his caudal region, while raising her head upwards about 30° by means of his pectoral held under her chin. During each such mating of about 2 sec duration a few eggs were extruded. The development of tubercles and swellings on the male pectoral fins is apparently related to this spawning behaviour.

In Alberta pearl dace are a significant forage fish, and are used by anglers as bait.




MYLOCHEILUS
CAURINUS
0 MILES 400
0 KILOMETRES 600

PEAMOUTH

Mylocheilus caurinus (Richardson)

Mylocheilus means *grinder lip* and *caurinus* means *of the northwest (wind).* The French common name for this species is *méné deux-barres.*

Distinguishing Characters

The small barbel at the corner of the mouth, the well-developed pelvic axillary process, the forward position of the dorsal fin, the deeply forked tail, and the small mouth that never extends back as far as the front of the eye.

Description

Body elongate, somewhat compressed; head small, less than one-quarter standard length; eye moderate, about one-half snout length (except in small specimens). Mouth small, oblique, slightly overhung by snout, never extends back to the front margin of the eye; pharyngeal teeth hooked in young, developing blunt and grinding surfaces in adults, usually 1,5–5,1 but occasionally 2,4–5,2 or 2,5–4,2; small barbel at corner of mouth, tiny in young. Branchiostegals 3 + 3; gill rakers short, best developed near the angle of the arch, a total of 8–12. Dorsal fin originates slightly in front of, or opposite, the origin of the pelvic fins; 8 major dorsal rays; 8 major anal rays; 14–18 pectoral rays (14–16 in our area); and 7–9 pelvic rays (8 in our area). Pelvic axillary process well developed (Fig. 21). Tail deeply forked, the middle rays shorter than or about equal to half the longest rays. Scales small, cycloid, 66–84 pored scales in the complete lateral line (68–84 in our area). Vertebrae 42–48 (45–48 in 27 fish from our area, including the 4 elements of the Weberian region). Intestine short, double looped.

Size: To 35 cm (14 inches).

Sexual dimorphism: Breeding males have small tubercles on the head, back, and dorsal, pectoral, and pelvic fins. In females these tubercles are reduced or absent, particularly on the fins. The backs of breeding fish are dark green in males, brown in females. The dark lateral stripes, and red colour, are more pronounced in males than in females. The pectorals are longer and darker in males than in females.

Colour: Back dark brownish or greenish, belly silver. Two dark lateral stripes, the upper extending to the tail, the lower ending opposite the vent. Breeding fish with red lips and an irregular red band across the cheek and along the flank below the lower dark lateral stripe. Young with a single narrow dark midlateral stripe only on the posterior half of the body; fins immaculate.

Distribution

On the Pacific Slope, from the Nass River to the Columbia River systems, and on Vancouver Island and some smaller inshore islands. East of the Continental Divide, in the Peace River system in British Columbia, and from the Athabasca River at Athabasca, Alberta.

Taxonomic Notes

The peamouth was originally named from the Columbia River as *Cyprinus (Leuciscus) caurinus* by Richardson in 1836. *Mylocheilus lateralis* is a synonym. There are no other species known in the genus.

From south to north, the peamouth shows a trend towards lower pectoral and pelvic fin ray counts, and perhaps towards higher scale and vertebral counts, but without any evident break such as might justify separation into different subspecies.

Postglacial Dispersal

The range of the peamouth includes only one glacial refuge, the Pacific. The populations in our area were derived by postglacial dispersal north from the Columbia system into the Fraser River, and from the Fraser system east across the Continental Divide into the upper Peace and Athabasca rivers (Mackenzie system).

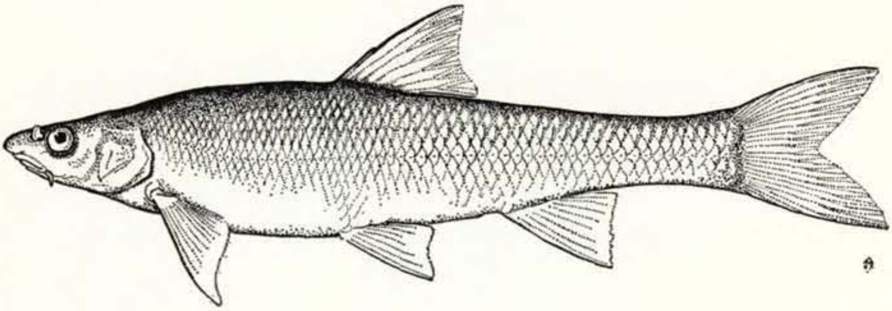
Biology

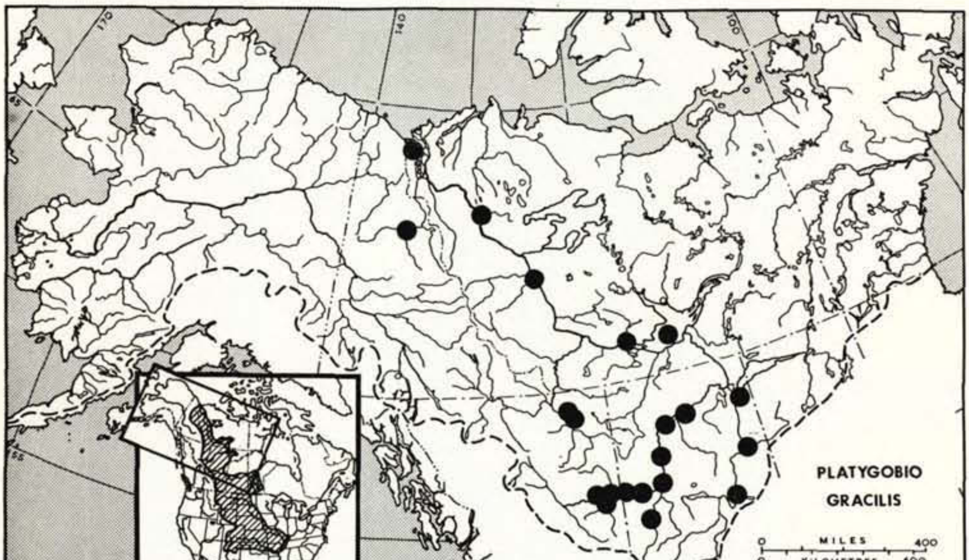
Peamouth occur both in lakes or in rivers, where both young and adults tend to remain in schools. In southern British Columbia lakes young peamouth occupy shallower water; adults remain close to the bottom in deeper water during daylight (except when spawning), and move into the shallows at night (Northcote et al., 1964). Large fish feed on aquatic and terrestrial insects, plankton, sometimes molluscs, and occasionally small fish.

This is one of the very few species of the family Cyprinidae that can tolerate salt water. Live peamouth have been taken several times near Vancouver in water less salty than the open ocean (due to influence of the Fraser River), but nonetheless distinctly marine. This tolerance accounts for the fact that peamouth are the only native cyprinids to successfully colonize Vancouver Island and other coastal islands.

Spawning takes place either in inlet or outlet streams close to a lake, or over gravel in the shallows of lakes. Dense spawning aggregations may form, within which an observer can easily distinguish the sexes by their colour differences. Large numbers of small greenish-grey adhesive eggs are shed and abandoned. Spawners were captured in a tributary to Summit Lake, Parsnip River drainage, in the 3rd week of May. Throughout British Columbia the spawning period varies from mid-May to early June. Eggs hatch in 7 or 8 days at 12 C (54 F).

Peamouth will take either bait or artificial fly, and are said by D. S. Jordan to possess considerable game qualities, often fighting continuously until brought to net. In former days they were served as food in some hotels in the Columbia basin.




PLATYGOBIO
GRACILIS
0 MILES 400
0 KILOMETRES 600

FLATHEAD CHUB

Platygobio gracilis (Richardson)

Platygobio means *flat gudgeon* (a European fish) and *gracilis* means *slender*. The French common name for this species is *méné à tête plate*.

Distinguishing Characters

The large barbel at the angle of the large mouth, the wide flat head, and the sickle-shaped fins.

Description

Body slender, somewhat compressed; head moderate, about one-quarter standard length, very wide and flat; eye small, about one-half snout length. Mouth large, slightly oblique, overhung by snout, upper jaw extends back to front margin of the eye; barbel well developed, somewhat longer than half diameter of the eye, placed at end of maxilla; pharyngeal teeth 2,4–4,2 or rarely 2,4–4,3. Branchiostegals 3 + 3; gill rakers short, a total of 4–6. Dorsal fin originates opposite or slightly in front of the origin of the pelvic fins; 8 major dorsal rays; 8 or 9 major anal rays; 14–20 pectoral rays (usually 16–19 in our area); and 8 pelvic rays. Pelvic axillary process well developed (Fig. 21). Pectoral, dorsal, and anal fins long and sickle-shaped, the outer pectoral ray longer than the third. Scales large, cycloid, 42–59 pored scales in the complete lateral line (usually 50–58 in our area). Vertebrae 40–47 (including the four Weberian elements), usually 44–47 in our area. Intestine short; peritoneum silvery below and dusky above.

Size: To 317 mm (12.5 inches).

Sexual dimorphism: Breeding males develop small tubercles on the top of the head and snout, on the anterior body scales, on the upper faces of the pectoral fin rays, and on the anterior rays of the dorsal, anal, and pelvic fins. In females these tubercles may be present on the head but are absent or very weakly developed elsewhere. In fish of comparable size the pectorals reach farther back in males than in females, but the relative lengths of the fins vary considerably with size.

Colour: Adults are dusky above, silver on the sides, and pale below. All fins are immaculate. Sometimes an indistinct dusky stripe is present on the posterior midline of the body. Young specimens are similar in colour to adults except that the midlateral stripe is more pronounced, especially posteriorly, and there is usually a distinct dark pigment spot at the base of the caudal fin.

Distribution

The Mackenzie River system, the Saskatchewan River system east to Lake Winnipeg, the basin of the Missouri River, and the Mississippi River south to Arkansas, and headwaters of the Rio Grande system in New Mexico. In our area, throughout most of the Mackenzie River north to its delta, but not upstream of Hudson Hope on the Peace River nor upstream of the Liard Canyon.

Taxonomic Notes

The flathead chub was first described from the Saskatchewan River at Carleton House by Richardson in 1836 as *Cyprinus (Leuciscus) gracilis.* The generic names *Pogonichthys* and *Hybopsis,* and specific or subspecific names *communis, pallidus, gulonellus, physignathus,* are amongst the names used for *Platygobio gracilis.*

The recent tendency towards consolidation of many cyprinid species into large genera has centred around the genus *Hybopsis* into which both *Platygobio gracilis* and *Couesius plumbeus* have been placed by some authors (Bailey, 1956; Hubbs and Lagler, 1964).

In Jordan and Evermann's treatise on North American fishes (1896), the genus *Hybopsis* was described as having never more than one pharyngeal tooth in the lesser row (counts 4–4, or 1,4–4,0, or 1,4–4,1). *Platygobio* and *Couesius* were distinguished from *Hybopsis* because they had rarely fewer than two pharyngeal teeth in the lesser row (counts 2,4–4,2). Since then, the genus *Hybopsis* was first split into several genera that had formerly been recognized only as subgenera (e.g., *Nocomis,* *Erimystax*) (Jordan et al., 1930; Hubbs and Lagler, 1949), and later was again consolidated into the single genus *Hybopsis*. These changes reflected different views of the nature of the generic category rather than new published information. A clear argument in favour of the expanded genus as a useful indicator of relationships is given by Rosen and Bailey (1963).

The return to the genus *Hybopsis* of those species whose close relationships have been generally acknowledged may well be justifiable. However, no reasons have been published for further expanding the genus *Hybopsis* to also include *Couesius* and *Platygobio*. Clearly Jordan and Evermann's characterization of the genus according to pharyngeal teeth would have to be abandoned, and no new description has been provided. If *Platygobio* be included in *Hybopsis* (with which it shares several characters) then the range of pharyngeal counts in *Hybopsis* would of necessity be expanded and would then encompass those of *Couesius*. But some of the characters of *Couesius* are shared with *Semotilus* rather than with *Hybopsis* (a small nonterminal barbel, sometimes high scale count, sometimes high gill-raker count). By redefining the genera, *Couesius* could justifiably be lumped with *Semotilus* instead of *Hybopsis*.

Since the relationships of *Platygobio* and *Couesius* to other groups is still unclear, they are best retained as separate genera until a review of the whole problem is available.

Two subspecies have been recognized, *Platygobio gracilis gracilis* (Richardson) and *Platygobio gracilis gulonellus* (Cope). The former occupies the northern part of the range and the Missouri–Mississippi River; the latter occupies the Arkansas River and Rio Grande drainages and some smaller streams on the Great Plains. Olund and Cross (1961) demonstrated higher scale, vertebral, and pectoral ray counts in the northern form, as well as differences in size and shape of body and fins. They concluded that these warranted subspecific recognition. Bailey and Allum (1962) showed that vertebral count in South Dakota specimens was inversely correlated with water temperature, and interpreted this as suggesting nongenetic modification of vertebral number. They did not recognize subspecies. Metcalfe (1966) suggests that the *H. g. gracilis* form inhabited the preglacial northward-flowing Missouri River tributary to Hudson Bay (Fig. 1), where it developed a different morphology and a preference for cooler water. Such a cold-tolerant form failed to enter the Mississippi or the Red River of the North during glaciation. Instead it survived only in the western Missouri River headwaters, and subsequently spread north into Canada. According to this hypothesis, present differences within the species have a hereditary, not a purely environmental basis.

Vertebral, scale, and pectoral ray count in specimens from our area all lie at the upper end of the ranges of variation for the species. Therefore, if subspecies are recognized, ours are *Platygobio gracilis gracilis* (Richardson).

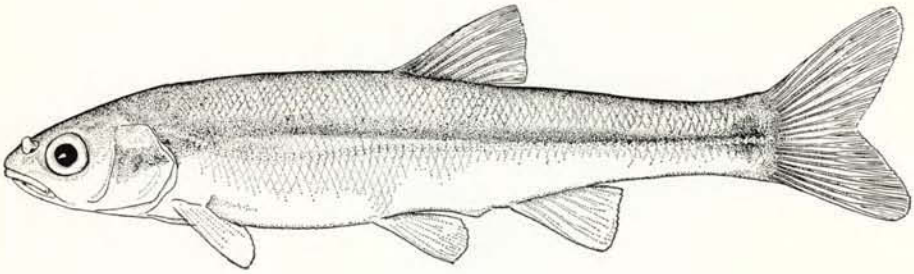
Postglacial Dispersal

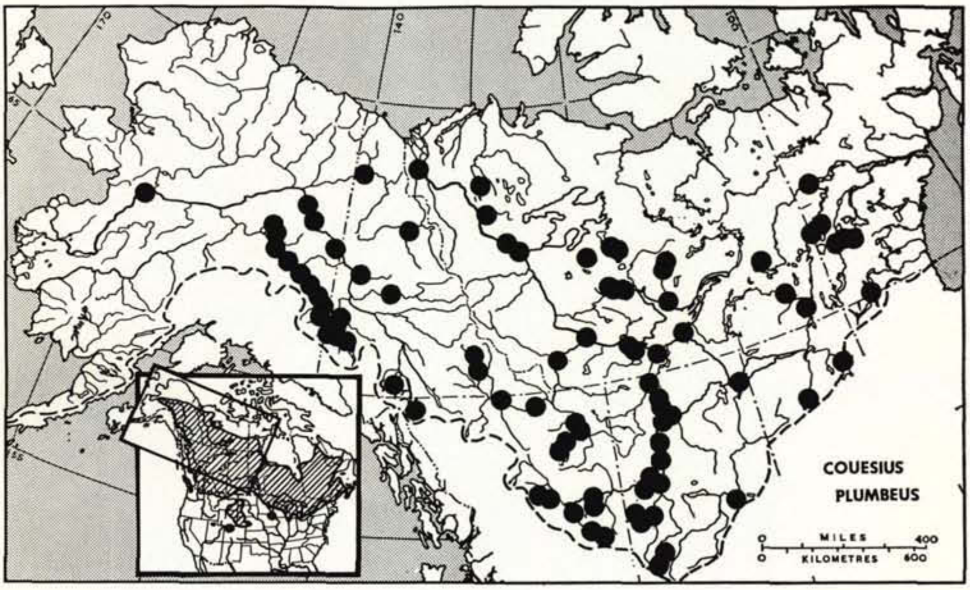
The range of the flathead chub includes only one glacial refuge, the Mississippi. However, the absence of *P. gracilis* from the upper Mississippi Valley and the Great Lakes indicates that it survived glaciation not in the upper Mississippi Valley but in the Missouri system and possibly in other large Mississippi tributaries farther to the south. The populations in our area were derived through postglacial dispersal northward from the Missouri system. It may have reached the Lake Winnipeg area after drainage of Lake Agassiz; otherwise it might be expected to have entered the Lake Barlow-Ojibway basin and perhaps the Great Lakes. Preglacial distribution has been discussed in the foregoing section.

Biology

The flathead chub has a distribution pattern unusual amongst northern cyprinids, in that it extends neither to the Pacific slope nor to the Great Lakes drainages. It is superbly adapted for life in muddy rivers of the plains, and is scarcely ever taken in standing or clear water. Its physiognomy is sharklike, and its feeding habits somewhat comparable; its eyes are small, but it has well-developed sensory barbels, and in the muddy water probably locates its food largely by smell. Its long sickle-shaped fins, flat wedge-shaped head, and flat belly all adapt it to swift current. Its mouth is large, and it is a voracious and omnivorous feeder. Stomachs of northern specimens have variously contained masses of stonefly or other aquatic insect larvae, terrestrial insects, sand, berries, seeds, feathers, young suckers, small spiny-rayed fish, and even a young rodent. At Old Fort Nelson in northern British Columbia numbers of flathead chub are enticed by the Indians into water so shallow that their dorsal fins project, attracted by a small sack of mixed soap flakes and dog food. The fish are then caught by baited hooks held against the sack, and are later boiled into a sort of stew. This sport is widespread; Preble (1908), describing the flathead chub in the Athabasca region, writes "It congregates in the eddies close to the bank and swims slowly along with the top of its head nearly flush with the surface. It is readily caught with a baited hook, and its capture is a favourite amusement with the Indian women and children when the boats are tied up to the bank. Being slender and bony, it is but an indifferent food fish." Sir John Richardson (1836) wrote of the "Saskatchewan dace" being taken at Carlton House in nets during the summer. Nowadays in Lake Winnipeg occasional specimens are taken by commercial fishermen, and some are angled on an artificial fly.

Little is known of the life history or breeding habits in our area. Spawning was probably in progress on June 27 in the Mackenzie River at 64°N, for some females taken then had large ovaries of almost free eggs, and one was spent. Spawning had probably ceased before August 4 in the Peace River at Fort Vermilion, as females taken then were spent. Olund and Cross (1961) believe that fish mature at about 85 mm standard length (3.3 inches). Flathead chub probably live for several years, as several size groups are present in some collections. The largest known specimen, from the Peel River at 66°N, had a total length of 317 mm (12.5 inches), much larger than most other northern cyprinids.





COUESIUS
PLUMBEUS
MILES
400
KILOMETRES
600

LAKE CHUB

Couesius plumbeus (Agassiz)

Couesius is named after Dr Elliot Coues, ornithologist, and *plumbeus* means *lead coloured.* The French common name for this species is *méné de lac.*

Distinguishing Characters

The distinct barbel not quite at the end of the upper jaw, the absence of a pelvic axillary process, and the origin of the dorsal fin slightly behind the origin of the pelvic fins.

Description

Body slender; head short, usually a little less than one-quarter standard length in mature specimens but larger in young fish; eye moderate, about 4 into head; snout short, broad, about 3.5 into head. Mouth moderate, slightly oblique, upper jaw extends back almost to the front margin of the eye, snout often projects slightly beyond mouth; barbel well developed, not quite at posterior end of maxilla (Fig. 23); pharyngeal teeth usually 2,4–4,2 but variable (0,4–4,0 and 2,5–4,2 are the extremes from our area). Branchiostegals 3 + 3; gill rakers short, a total of 4–9 (usually 5–7 in our area). Dorsal fin originates slightly behind origin of pelvic fins (except in young, in which the two points may be opposite); 8 major dorsal rays; 8 major anal rays; 17–19 pectoral rays; and 8 pelvic rays. Scales moderate, cycloid, 53–79 (usually 58–65 in our area) pored scales in the complete lateral line. Pelvic axillary process absent in our area, but present in some eastern specimens. Vertebrae 39–44 (including the 4 elements of the Weberian region). Intestine short, one loop; peritoneum silvery with dark speckles.

Size: To 152 mm (6 inches), but usually less than 10 cm (4 inches) long.

Sexual dimorphism: Breeding males develop fine tubercles on the head and on the scales just behind the head, and also on the top surface of the first 9 or 10 rays of the pectoral fin. There are also tubercles on the dorsal surface of the first and second rays of the pelvic fins, but no tubercles, or only a very weak one, on the dorsal and anal fins. In females the tubercles are present but very weakly developed. The paired fins of males are much longer than those of females; the pectorals extend more than two-thirds of the distance back towards the pelvics in breeding males, but not in females. In populations west of the Continental Divide breeding males develop an extremely rough patch of tubercles just in front of each pectoral fin. It is not known whether this patch of tubercles is developed on breeding males of the Mississippi form of *C. plumbeus.*

Colour: Adults are dark brown or green above and pale below, with an indistinct dark midlateral band on the back half of the body. The fins are immaculate except for some dusky pigment on the dorsal surface of the pectoral fins. In young fish (to 2 inches long) the dark midlateral stripe is much more prominent and sometimes extends forward onto the head and in front of the eye. Breeding males of the Mississippi form of *C. plumbeus* (see "Taxonomic Notes") develop distinct red patches on the inner base of the pectoral fins. These red patches are absent in breeding males of the Pacific form.

Distribution

From the Yukon and Mackenzie River systems, south on Pacific coast drainages as far as the upper Fraser and upper Columbia systems, widespread across Canada to Ungava and Nova Scotia, south to northern New England and the Great Lakes, with isolated populations in the upper Mississippi system in Iowa, and in the Dakotas, Nebraska, Montana, Wyoming, and Colorado. In our area, throughout the Yukon River system as far downstream as Nulato; throughout the Mackenzie system north to the delta; extending into the Barren Grounds in Anderson River and in tributaries to Chesterfield Inlet, Thelon, Dubawnt, and Kazan rivers, and Nueltin Lake.

Taxonomic Notes

The lake chub was first described as *Gobio plumbeus* by Agassiz in 1850. *Couesius greeni* from British Columbia and *Couesius* (originally *Leucosomus*) *dissimilis* from Montana are not now considered to be species distinct from *Couesius plumbeus.*

Couesius plumbeus has been referred to as *Hybopsis plumbea* by several recent authors. Reasons against lumping the genera *Couesius, Platygobio,* and *Hybopsis* have been presented in the "Taxonomic Notes" for *Platygobio gracilis.*

Within our area there appear to be at least two allopatric morphological forms of the lake chub. The characteristics most useful in separating them are the number of scales around the caudal peduncle and the number of vertebrae. Throughout the Yukon system, most of the Mackenzie system, and onto the Barren Grounds, there is a form characterized by high mean caudal peduncle scale counts (21.5–23.7) and high mean vertebral counts (41.5–42.3). This form is also found in the Great Lakes, New England, and the Missouri system. The form *dissimilis* (which according to Hubbs and Lagler (1964) may represent a distinct species) occurs in Michigan and perhaps westward to Colorado. On the west side of the Continental Divide in the Columbia and Fraser systems is a form characterized by low mean caudal peduncle scale counts (18.8–20.8) and also low mean vertebral counts (40.5–40.7). This form is also found in the upper Peace River (Mackenzie system) above the Peace Canyon. Development of colour and of tubercles in breeding males may also differ between the two forms, which probably arose during isolation in separate glacial refuges. But, although morphological variation suggests a Pacific refuge, the restricted distribution within the Columbia system is puzzling.

Status of subspecific names in *Couesius plumbeus* have been discussed by Lindsey (1956, p. 769). If subspecies be recognized, then both *Couesius p. plumbeus* and *Couesius plumbeus greeni* probably occur in our area.

Postglacial Dispersal

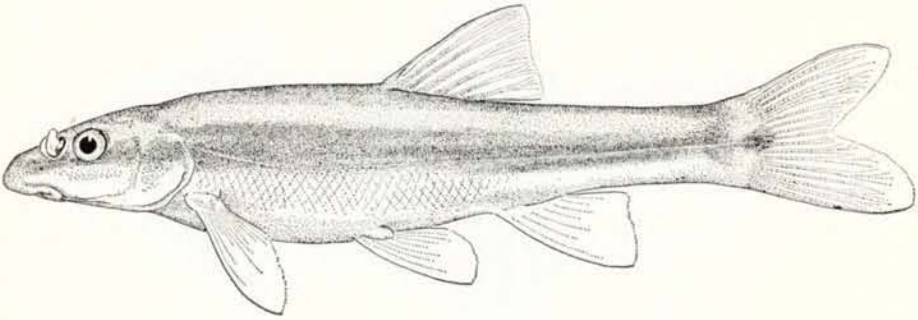
The range of the lake chub suggests at least three possible glacial refuges: the Bering, the Pacific, and the Mississippi (and possibly also an Atlantic refuge). The presence of two allopatric morphological forms in our area indicates that our lake chub populations were derived from at least two separate refuges. In the unglaciated portions of Alaska the lake chub is confined to the Yukon River and its tributaries. If *Couesius* had survived glaciation in the Bering refuge it would probably be more widespread there. Lake chub in the Yukon system are morphologically similar to those in the Mackenzie system, and probably entered the Yukon from the Mackenzie postglacially. The distribution of the two morphological forms in our area suggests survival in the Pacific and Mississippi refuges. The Pacific form probably survived glaciation in the Columbia system and postglacially expanded its range northward to the Fraser River, and from there eastward into the upper Peace River (Mackenzie system). In the Mississippi refuge *Couesius* is present in the upper Missouri system, and occurs as relict populations in South Dakota, North Dakota, Nebraska, Colorado, and Iowa. The relict Iowa population is the only record for the upper Mississippi River. The Mississippi form of *Couesius* probably entered our area through postglacial dispersal from the upper Missouri system.

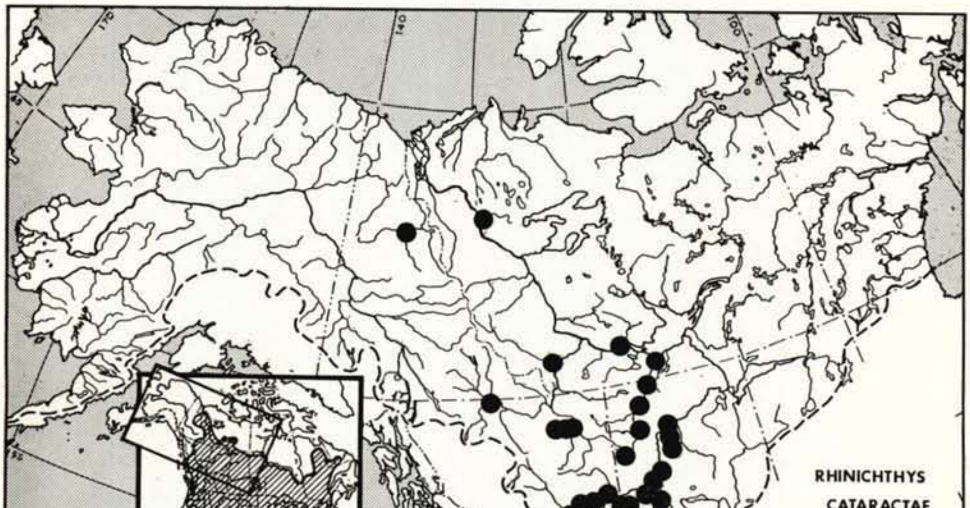
Biology

The lake chub tolerates a wide variety of environments, and has the most widespread northern distribution of any North American cyprinid. It frequents lakes and streams including both clear and very muddy waters, and even the outlets of hot springs (including the lower pools of Liard Hot Springs on the Alaska Highway and springs near Atlin Lake). It sometimes occurs in large schools. Stomach contents include terrestrial and aquatic insects, zooplankton, and algae; some specimens from our area had eaten small fish. In small lakes in central British Columbia the lake chub remains close to the bottom regardless of depth, occupying the deepwater bottom zone as well as inshore areas except in lakes that lack oxygen in deep water during summer. In central British Columbia fish mature in their 3rd or 4th year, and probably seldom survive beyond 5 years. Females grow faster and live longer than males (G. H. Geen, personal communication).

Spawning has not been observed in our area, but commences in some lake outlets in the Cariboo district of central British Columbia in late May or early June. Females with ripe or near-ripe eggs have been taken in southern Yukon Territory in late May; ripe females and males with well-developed tubercles occur in far northern collections taken as late as August. The eggs are yellow when laid. At Lac la Ronge, Saskatchewan, lake chub were observed spawning amongst and underneath large rocks in the shallows of the Montreal River, in middle or late May (J. H. Brown, personal communication). No nest was constructed, and parents did not guard the eggs.

The lake chub probably serves as an important article of diet for larger fish in some northern lakes that contain few species of small forage fish, particularly where it converts organisms from the bottom in deeper water into food more readily available to piscivorous species.





RHINICHTHYS
CATARACTAE
MILES
KILOMETRES
0
400
0
600
170
140
100

LONGNOSE DACE

Rhinichthys cataractae (Valenciennes)

Rhinichthys means *snout fish* and *cataractae* means *of the cataract* (first taken at Niagara Falls). The French common name for this species is *naseux de rapides.*

Distinguishing Characters

The presence of a barbel, the long overhanging snout, and the absence of a groove between the upper lip and tip of snout.

Description

Body slender, somewhat flattened anteriorly; head large, about 3.5 into standard length; eye very small, about 5 or 6 into head; snout long, overhanging, about 3 into head. Mouth moderate, almost horizontal, lips thick, almost suckerlike, the upper lip attached to snout with no intervening groove (Fig. 20), mouth not reaching front margin of eye; barbel well developed and at end of maxilla; nostril flaps large and conspicuous; pharyngeal teeth usually 2,4–4,2 but occasionally only one tooth on either inner row. Branchiostegals 3 + 3; gill rakers short, a total of 5–8. Dorsal fin originates behind the origin of the pelvic fins; 8 major dorsal rays; 7 major anal rays; 14 or 15 pectoral rays; and 8 or 9 pelvic rays. Pelvic axillary process well developed. Scales small, cycloid; 58–76 pored scales in the complete lateral line (usually more than 60 in our area). Vertebrae 40–42 (including the 4 Weberian elements). Intestine short; peritoneum silvery with dark speckles; gasbladder often short and narrow.

Size: Recorded up to 152 mm (6 inches) in length, but usually less than 101 mm (4 inches) long.

Sexual dimorphism: Breeding males develop small tubercles on the top of the head and on the dorsal surface of the pectoral and pelvic fins, as well as on the anal and dorsal fins.These are absent or only weakly developed in females. The paired fins are longer in males than in females.

Colour: Adults are olive to dark green or black on the back and light below. An indistinct, dark midlateral stripe extends from the gill cover to the base of the caudal fin. In some populations this stripe is absent, and in others it is present only on the back half of the body. The fins are usually immaculate, or with a slight dusky tone (particularly the caudal fin). In breeding males a distinct light leading edge followed by a patch of darker pigment develops on the paired fins. East of the Continental Divide breeding males may develop reddish colouration bordering the upper lip and at the base of each of the lower fins; west of the Divide this colour is faint or absent. The young are generally lighter than adults, and the midlateral stripe is very pronounced. It begins in front of the eye and ends at the base of the caudal fin with an abrupt constriction followed by a small more intensely pigmented spot. In young fish (up to about 2 inches) there is a band of dark pigment at the midbase of the dorsal fin.

Distribution

On the Pacific slope south from the Skeena to the Columbia River systems. From the Mackenzie system east to Labrador and Montreal, south to North Carolina, Iowa, and Mexico. In our area, throughout the Mackenzie River including its upper tributaries, north almost to the Arctic Circle.

Taxonomic Notes

The longnose dace was first described from Niagara as *Gobio cataractae* by Valenciennes in 1842. Synonyms include the specific or subspecific names *dulcis, nasutus, maxillosus,* and others. This wide-ranging and variable species forms a series of geographic races whose subspecific status is in doubt. Breeding colouration and perhaps other characteristics may differ between populations in Canada east and west of the Continental Divide, but these await study.

Postglacial Dispersal

The longnose dace has the widest distribution of any North American cyprinid. This range includes three possible refuges: the Pacific, the Mississippi, and the Atlantic. The longnose dace is widely distributed in these areas and probably survived glaciation in all three. It is unlikely that the Atlantic refuge contributed to the northern distribution of *R. cataractae.* The populations in our area were probably derived mainly from the Mississippi refuge, with the exception of the populations in the upper Peace River that may have had a Columbia (Pacific refuge) origin.

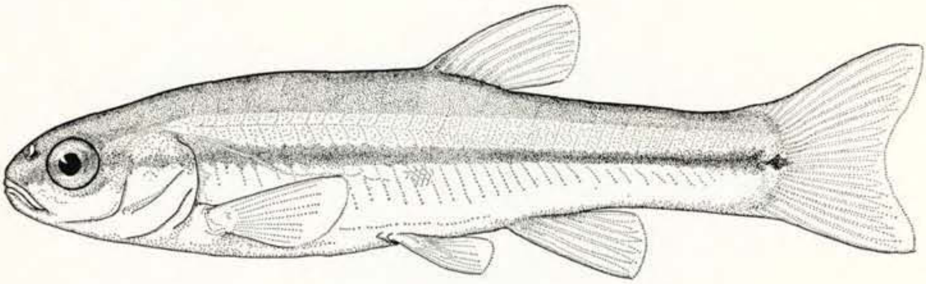
Biology

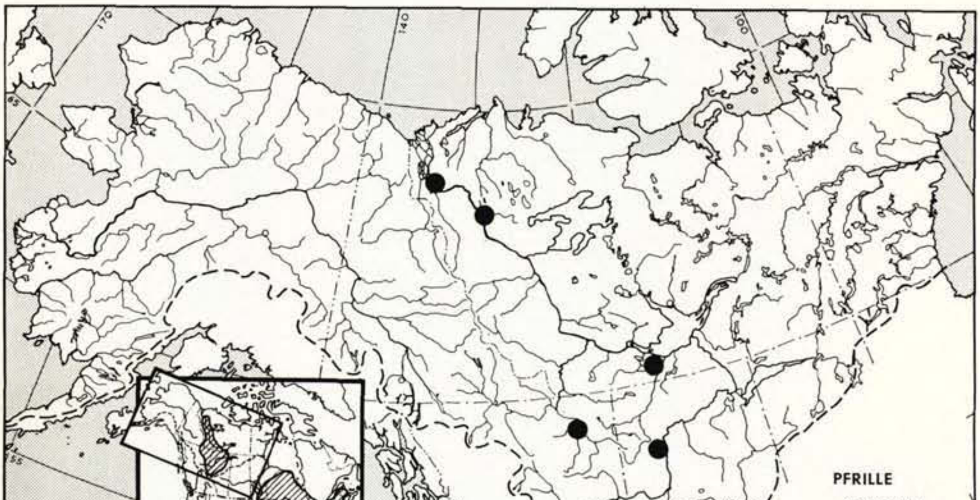
Longnose dace are bottom dwellers, found usually in running water, either clear or muddy. Gee and Northcote (1963) showed that the gasbladder does not increase in size to keep pace with body growth, so that larger fish have relatively smaller gasbladders, and are consequently less buoyant. The older (and heavier) fish move out into swifter current, and may as adults live in crannies between stones in very fast water (as much as 6 ft/sec surface velocity). They are therefore difficult to capture, but may be taken by overturning stones in swift water and displacing the dace into a net held below. They are solitary rather than schooling fish. Gasbladder volume of adults varies between different populations; recent experiments by J. H. Gee (personal communication) demonstrate that buoyancy can be altered voluntarily in response to current.

Spawning has not been observed in our area, but in central British Columbia it occurs in June and early July; in Kannanaskis Lake, Alberta, it may continue until late August.

Probably no nest is constructed, but the male guards a territory. Eggs are laid in a group down amongst stones, and are probably guarded by one parent. In Manitoba, females lay from 200 to 1200 eggs, which are adhesive, transparent, and so colourless as to be almost invisible under water. These hatch in 7–10 days at 16 C (60 F). The yolk sac is absorbed about 7 days later; the young then rise to the surface and inflate the posterior lobe of the gasbladder with air. They then become pelagic, living in still shallow water at the river margin. After about 4 months they begin selecting faster current, and gradually move into deeper water (J. H. Gee, personal communication). Sexual maturity probably occurs in their 3rd year.

The few stomachs examined from our area contained principally aquatic insect larvae. Longnose dace are well adapted to feed on sessile insect larvae in fast water, and are known in southern areas to feed on blackfly larvae. Their contribution to control of blackfly populations near running water has not been investigated.




PFRILLE
NEOGAEA
0 MILES 400
0 KILOMETRES 600

FINESCALE DACE

Pfrille neogaea (Cope)

Pfrille is the German colloquial name for the European minnow *Phoxinus phoxinus,* and *neogaea* means *new world.* The French common name for this species is *ventre citron.*

Distinguishing Characters

The absence of a barbel, the small scales (more than 55 in the lateral line), the single dark lateral stripe, the blunt snout, and the large mouth reaching the anterior margin of the eye.

Description

Body robust, somewhat compressed; head large, broad, and blunt, about 3 into standard length; eye small, less than snout. Mouth large, oblique, extending back almost to the front margin of the pupil. Upper and lower lips even, sometimes projecting slightly beyond the snout. Pharyngeal teeth 2,5–5,2 or 2,5–4,2. Branchiostegals 3 + 3; gill rakers short, a total of 7–10. Dorsal fin far back, its origin behind the origin of the pelvic fins, and the posterior end of its base behind the origin of the anal fin; 8 or 9 major dorsal rays; 8 or 9 major anal rays; 13–16 pectoral rays; and 7 or 8 pelvic rays. No pelvic axillary process. Peduncle deep, its depth about equal to dorsal fin base. Scales small, cycloid, embedded in large specimens; 67–85 scales along the midlateral line; 9–34 pored scales in the incomplete lateral line, which does not extend beyond the dorsal fin base. Vertebrae 37–40 (including the 4 Weberian elements). Intestine short, not lying in coils beneath the stomach; peritoneum dark brown or black.

Size: To 76 mm (3 inches).

Sexual dimorphism: The pectoral fins of breeding males are noticeably modified; the first pectoral ray develops a heavy splintlike thickening on its anterior surface extending from the base along about one-quarter of the ray, where it ends abruptly to form a distinct notch on the leading edge of the fin. The upper pectoral rays are thickened and the membranes between are swollen. None of these modifications occurs in females. The pectoral tips extend more than half way back to the pelvic fin bases in males but not in females. Breeding males also develop tubercles on the scales at the base of the anal fin.

Colour: Back black or dark bronze, belly cream or white. A dark lateral stripe extending onto the tail base where it becomes narrower and darker. A pale stripe above this midlateral dark stripe. Pale parts of breeding males reported to be yellow by some authors, crimson by others. Males taken from Pierre Gray Lake, Alberta (past the breeding season), had light yellow underparts, and a red band beneath the dark lateral stripe. In the young the dark stripe is pronounced.

Distribution

From the Mackenzie River to New Brunswick, south to the Adirondack region, Minnesota, and Wisconsin (including one record from the Mississippi drainage); also isolated populations in South Dakota, Nebraska, and Wyoming. In our area, throughout the Mackenzie River system as far north as the Arctic Circle, but not in the upper Liard or upper Peace River basins.

Taxonomic Notes

This species was originally named from Michigan as *Phoxinus neogaeus* by Cope in 1869. The Old World genus *Phoxinus* has its greatest variety of species in Asia. One widespread and variable species, *Phoxinus phoxinus,* ranges from Spain to the Anadyr River (which enters the Bering Sea only 350 miles from Alaska). Close relatives might be expected in America, for at least in the Baltic *P. phoxinus* "does not avoid brackish waters" (Berg, 1948–49). In the New World, the range of *Pfrille neogaea* comes close to the Arctic Ocean in the lower Mackenzie River. Jordan and Evermann (1896, p. 241) and others have pointed out that *phoxinus* of Eurasia and *neogaea* of North America are closely allied, and *neogaea* conforms to all the characters of the genus *Phoxinus* as given by Berg (1949).

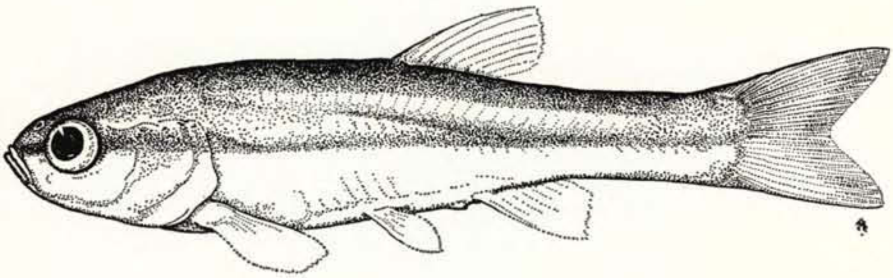
In 1951 Bailey proposed lumping *neogaea* in the New World genus *Chrosomus.* Reasons for this suggestion have not been published, but it appears to us that the case is stronger for placing *neogaea* in *Phoxinus* than in *Chrosomus.* The species has two rows of pharyngeal teeth and only a single intestinal loop, both of which are present in every species of *Phoxinus* and in no species of *Chrosomus.* Perhaps the genera *Phoxinus* and *Chrosomus* should be lumped. (*Phoxinus* has page priority over *Chrosomus,* both names appearing in Rafinesque (1820).) Such a move has been suggested by Banarescu (1964), but apparently without documentation. For the present, in the absence of a published revision based on all of the species involved, we follow Jordan (1924) in considering *neogaea* to be of uncertain affinity, best placed by itself in the genus *Pfrille.*

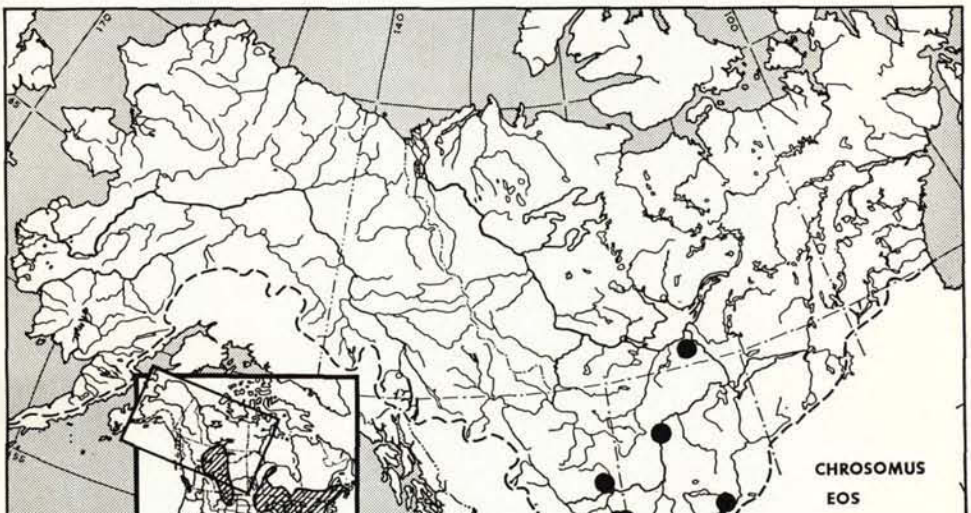
Postglacial Dispersal

The range of the finescale dace includes only one glacial refuge, the Mississippi refuge. At present *P. neogaea* is absent from the upper Mississippi and St. Croix rivers in Minnesota (Underhill, 1957), but is present as a relict in central Wisconsin. There are also relict populations in Nebraska and South Dakota. These indicate that *P. neogaea* survived glaciation in the Missouri system and perhaps in the lower Mississippi. Because of the timing and pattern of deglaciation the populations in our area were probably derived by postglacial dispersal northwards from the Missouri system. The lack of records from the Churchill and Saskatchewan river systems is puzzling, but may be due to lack of intensive collecting in suitable habitats.

Biology

The finescale dace is most often taken in cool boggy lakes or streams, but it has been collected from the margins of the large Fort Nelson River in northeastern British Columbia, and from the Mackenzie River at Fort Good Hope. Fish from three localities in our area had fed mostly on insects. Spawning, said to occur in June and July, has not been described, and the role played by the curiously notched pectoral fins in breeding males is unknown. The finescale dace often hybridizes with the northern redbelly dace *Chrosomus eos*; the hybrids are apparently most often females, but whether they are fertile is unknown (New, 1962). It is unfortunate that so little is known concerning this fish, which may form an unusual link between New World and Old World minnows.





CHROSOMUS
EOS
MILES
0
400
KILOMETRES
0
600

NORTHERN REDBELLY DACE

Chrosomus eos Cope

Chrosomus means *coloured body* and *eos* means *sunrise*. The French common name for this species is *ventre rouge du nord*.

Distinguishing Characters

The absence of a barbel, the very small scales, the double dark lateral stripes, and the coiled intestine and black lining of the body cavity.

Description

Body elongate, somewhat compressed; head moderate, about 3.5 into standard length; eye larger than snout. Mouth moderate, very oblique, somewhat S-shaped in side view, usually not reaching to front margin of pupil; pharyngeal teeth 5–5 or 5–4. Branchiostegals 3 + 3; gill rakers moderate 10–13, those near the angle of the arch well developed. Dorsal fin originates well behind the origin of the pelvic fins; 7 or 8 major dorsal rays; 8 or 9 major anal rays; 14–16 pectoral rays; and 8 or 9 pelvic rays. No pelvic axillary process. Peduncle deep, slightly deeper than base of dorsal fin (except in fish shorter than 1 inch). Scales very small, cycloid; 83–95 scales along the midlateral line; sometimes no pored lateral line scales, but usually up to 15. Vertebrae 37–40 (including the four elements of the Weberian region). Intestine long and coiled beneath the stomach, more than twice length of body; peritoneum dark brown to jet black.

Size: To 76 mm (3 inches).

Sexual dimorphism: The brilliant colouration of males during spring and summer is distinctive.

Colour: Back olive to dark brown, belly white or cream. Two dark lateral stripes, the upper less distinct, sometimes interrupted posteriorly. Lower stripe terminating in dark spot on caudal fin base, the spot about the same width and darkness as the stripe. Lower flanks and abdomen of males said to be brilliant red during spawning time, yellow immediately before and after. Lining of body cavity black. Young with only the lower dark lateral band distinct.

Distribution

From the Peace River eastward to Nova Scotia, southward to South Dakota and Nebraska, southern Wisconsin, southern Ontario, and the Adirondacks. The most westerly record is from Charlie Lake, B.C.; the most northerly is from Fuller Lake in Wood Buffalo Park, N.W.T. Hybrids *C. eos* × *Pfrille neogaea* are reported from Colorado (Bailey and Allum, 1962).

Taxonomic Notes

Chrosomus eos was first described from the Susquehanna River by Cope in 1862. The northern redbelly dace has sometimes been confused in the literature with *Chrosomus erythrogaster*, or referred to as a subspecies *Chrosomus erythrogaster eos*. However, *C. eos* and *C. erythrogaster* are apparently distinct species that occur together while retaining their identity in a narrow belt close to the southern limits of *C. eos*. Previous references to *C. erythrogaster* in Canada are probably all based on specimens of *C. eos*. *Chrosomus dakotensis* is a synonym of *Chrosomus eos*.

The New World genus *Chrosomus* apparently resembles the Old World *Phoxinus*, but whether this resemblance is superficial or fundamental cannot be known without thorough review of all the species involved.

Postglacial Dispersal

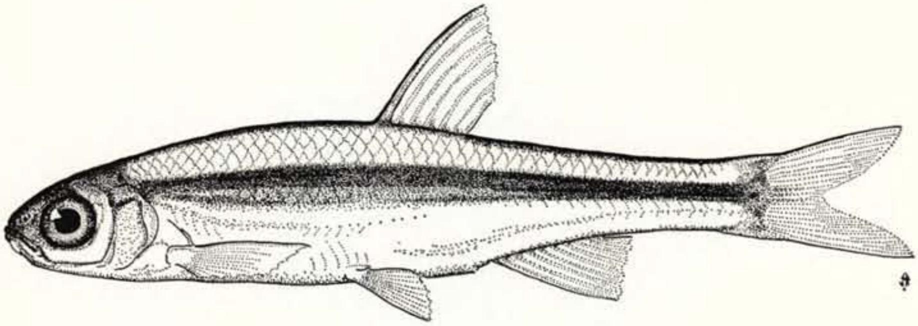
The range of the northern redbelly dace includes two glacial refuges, the Mississippi and Atlantic. The restricted distribution of *C. eos* in the Atlantic refuge (Susquehanna, Patapsco, and Potomac rivers) suggests a postglacial dispersal into that area from the Mississippi system via the Great Lakes. Even if *C. eos* also survived glaciation in the Atlantic refuge it is unlikely that any of the populations in our area were derived from that source. In the Mississippi refuge *C. eos* is known from scattered localities in the upper Mississippi system, and in the Missouri system from a few relict populations in Nebraska and South Dakota. There is also a relict population in northern Colorado. During the Wisconsin glaciation the northern redbelly dace was probably continuously distributed in the upper Mississippi and Missouri systems. Because of the timing and pattern of deglaciation, the populations in the Missouri system had the first opportunity to disperse northward.

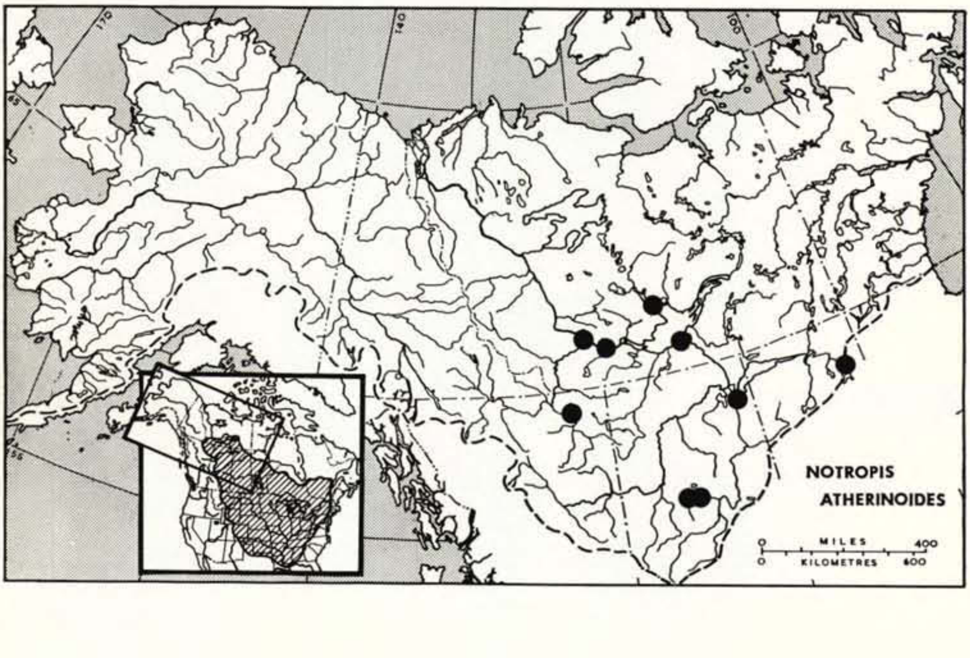
Biology

This little minnow occurs mainly around the boggy margins of small lakes. As might be surmised from its long coiled intestine and black peritoneum, it feeds largely on plant material; fish from our area have been found to contain masses of filamentous algae along with associated small invertebrate organisms. The species perhaps spawns more than once during the summer. Spawning has not been observed in our area, but some females taken on August 24 in Pierre Gray Lake in northern Alberta contained eggs that though white were quite large and rather free, although males did not show breeding colours.

In Michigan, males are vividly coloured during the spawning season from late May to August. Hubbs and Cooper (1936) describe breeding in Michigan as follows. When breeding, a female becomes active and attracts from one to eight males. She darts several feet through the water, pursued by males, and then drives headlong into a mass of filamentous algae, immediately followed by one or more males. A few non-adhesive eggs are fertilized and scattered amongst the filaments, after which the group, in courtship pursuit, darts from one algal mass to another, depositing eggs in each. In Michigan, the young emerge in from 8 to 10 days at temperatures from 70 to 80 F; maturity is reached in the 2nd or 3rd year.

Because the northern redbelly dace is largely a plant-feeder, it probably does not compete with sport fishes such as trout, and may in some lakes serve as forage fish.




NOTROPIS
ATHERINOIDES
MILES 400
KILOMETRES 600

EMERALD SHINER

Notropis atherinoides Rafinesque

Notropis means *back keel* (the original type specimen was shrivelled by drying) and *atherinoides* means *like the silverside*. The French common name for this species is *méné émeraude*.

Distinguishing Characters

The absence of a barbel, large scales, the long anal fin, and the backward placement of the dorsal fin. An iridescent and fragile-appearing fish.

Description

Body elongate, considerably compressed; head moderate, about one-quarter standard length; eye large, somewhat greater than snout in specimens over 38 mm (1.5 inches) long. Mouth small, terminal, oblique, extends back almost to the front margin of the eye; pharyngeal teeth usually 2,4–4,2. Branchiostegals 3 + 3; gill rakers moderate, a total of 9–12 on the first arch. Dorsal fin originates well behind origin of pelvic fins; 8 major dorsal rays; 9–13 major anal rays (usually 10 or 11 in our area); 13–15 pectoral rays; and 8 or 9 pelvic rays. Pelvic axillary process present. Scales large, cycloid, 35–43 pored scales in the complete lateral line (usually 40–43 in our area). Vertebrae 36–43 (including the 4 Weberian elements), usually 39–43 in our area. Intestine short; peritoneum heavily speckled.

Size: To 101 mm (4 inches) but usually 90 mm (3.5 inches) or less.

Sexual dimorphism: Breeding males (but not females) have very small tubercles on the upper surface of the pelvic fins. In the south, males in spring are said to have a rose-coloured snout.

Colour: Adults are an iridescent silvery-green to bluish-green above and silvery-white below. There is usually a distinct emerald green or metallic silvery midlateral band and a narrow mid-dorsal stripe. The fins are transparent except for some white on the anal fin and lower lobe of the caudal fin. Young specimens (up to 2 inches) are somewhat translucent.

Distribution

From the lower Liard River (Mackenzie system) east to Lake St. John and Lake Champlain, south (west of the Appalachians) to Alabama and the Trinity River, Texas. In our area, in Mackenzie River tributaries south from the junction of the Liard and Mackenzie rivers, including the Fort Nelson River in British Columbia; not recorded from the Peace River.

Taxonomic Notes

The emerald shiner was originally named from Lake Erie by Rafinesque in 1818 as *Notropis atherinoides. Notropis dilectus* is a synonym. Hubbs and Lagler (1958) recognize two subspecies of *Notropis atherinoides*, and believe that the southwestern *Notropis percobromus* (Cope) is a distinct species. Bailey and Allum (1962) and Cross (1967) lump all three forms, without subspecific designation. The range as stated here and shown on our map includes that of *N. percobromus.* If subspecies be recognized, our area contains *Notropis atherinoides atherinoides* Rafinesque.

Postglacial Dispersal

The range of the emerald shiner includes two possible glacial refuges, the Mississippi and Atlantic. The range in the Atlantic refuge is restricted to the Potomac River and drainages to the north. These Atlantic coastal plain populations are apparently morphologically similar to the Mississippi form, and probably were derived postglacially from the Mississippi refuge via the Great Lakes. In the Mississippi refuge *N. atherinoides* is widespread in the upper Mississippi and Missouri systems. Because of the timing and pattern of deglaciation the populations in our area were probably derived from the upper Missouri.

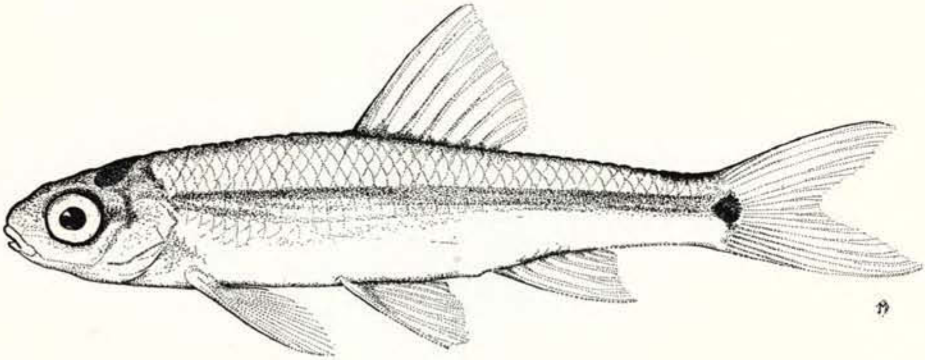
Biology

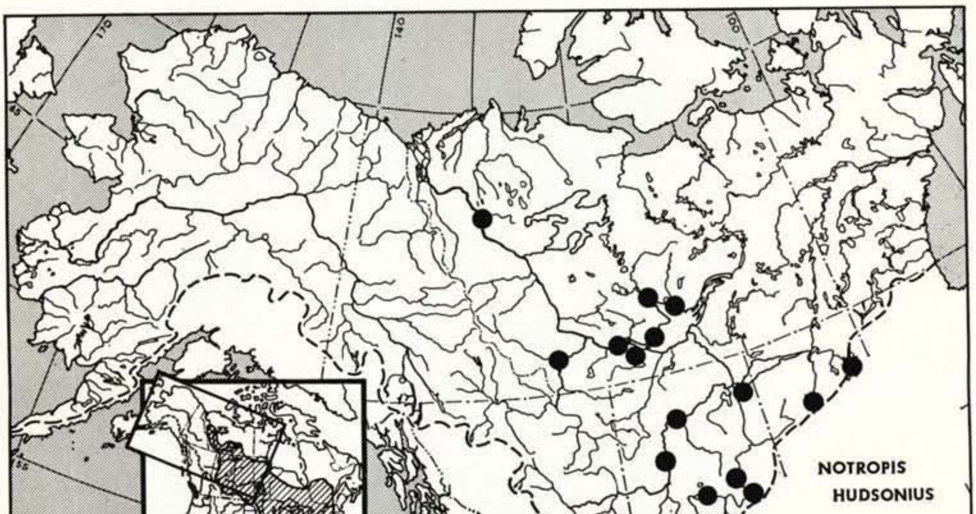
In our area the emerald shiner is found in lakes and in large rivers. It is pelagic in habit; in the south it is said to move about, sometimes in enormous schools, in the surface layers of the open water, in preference to the vicinity of weed beds. In Ohio lakes it habitually comes to the surface at night to feed. The few northern specimens examined had fed on plankton crustaceans or on insect larvae.

In South Dakota it is reported to feed primarily on zooplankton and to select the larger organisms, particularly *Daphnia.* Young-of-the-year change their diet with size, feeding first on blue–green algae and rotifers and later on green algae and crustacean plankton (Fuchs, 1967).

Spawning has not been observed in our area, but in the south it reportedly occurs in late spring and in summer, in shallow shore waters. Eggs hatch 24–32 hr after fertilization; fry at hatching are about 4 mm long. In South Dakota fish average 66 mm long at formation of the first annulus on their scales (in late spring), and 84 mm at formation of the second. Almost all fish over 60 mm long showed gonad development (Fuchs, 1967). Each fish may spawn more than once during the summer. Males grow more slowly and have a higher mortality rate than females. Only a few fish in their 4th year were encountered in South Dakota; populations were characterized by high mortality that caused drastic variations in age-class structure.

This is in some areas an important forage fish. It is used extensively in Ontario and elsewhere as bait, and is sold frozen, salted, or preserved in jars for use by anglers.




NOTROPIS
HUDSONIUS
0 MILES 400
0 KILOMETRES 600

SPOTTAIL SHINER

Notropis hudsonius (Clinton)

Hudsonius is named from the Hudson River, N.Y. The French common name for this species is *queue à tache noire.*

Distinguishing Characters

The absence of a barbel, the large scales, and the well-developed black spot at the base of the caudal fin.

Description

Body elongate, considerably compressed; head moderate, about one-quarter standard length; eye large, greater than snout; mouth small, slightly oblique, extends back almost to the front margin of the eye; pharyngeal teeth variable, but usually 2,4–4,2 in our area (occasionally 1,4–4,1 or 0,4–4,0). Branchiostegals 3 + 3, gill rakers short, a total of 5–7 on the first arch. Dorsal fin originates above, or slightly in front of, the origin of the pelvic fins; 8 major dorsal rays; 7 or 8 major anal rays; 14–16 pectoral rays; and 7 or 8 pelvic rays. Pelvic axillary process present. Scales large, cycloid, 36–41 pored scales in the complete lateral line (usually 36–40 in our area). Vertebrae 37–41 (including the 4 Weberian elements), usually 38 or 39 in our area. Intestine short; peritoneum silvery.

Size: To 152 mm (6 inches), but usually less than 127 mm (5 inches).

Sexual dimorphism: Breeding males, but not females, have small tubercles on the top of the head and on the upper pectoral rays. The pectorals reach over three-fourths the distance to the pelvic base in breeding males, but only about two-thirds the distance in females.

Colour: Adults are pale green to greenish-blue above, and white below. There is usually a bold black spot about one-half the size of the eye at the base of the caudal fin, and a distinct silvery band along the midlateral line. The fins are transparent except for a white ventral edge on the caudal fin. The young are similarly coloured.

Distribution

The species ranges from the Mackenzie River system east to Quebec, south along the Atlantic coast to the Ocmulgee River, Georgia, and west to Kansas. In our area it occurs throughout much of the Mackenzie system downstream to Good Hope, but is not recorded from the upper Liard nor the upper Peace River systems.

Taxonomic Notes

The spottail shiner was originally named from Hudson River as *Clupea hudsonia* by Clinton in 1824. The large genus *Notropis* has been variously divided into smaller genera or subgenera; moreover, the species *hudsonius* as now understood includes several forms at one time considered to be separate species. Some of the synonyms for *Notropis hudsonius*, therefore, are combinations of the generic names *Hudsonius, Luxilus, Cliola,* or *Opsopoedus* and the specific or subspecific names *fluviatilis, selene, scopiferus, scopifer, amarus, storeriana, saludanus, borealis,* and others. Our range statement and map inset include all of the forms of the species *Notropis hudsonius*. According to Hubbs and Lagler (1964) the subspecies in our area is *Notropis hudsonius hudsonius*, which is rather weakly separable but distinguishable from the subspecies occupying the Great Lakes and tributary waters other than Lake Superior; the northern subspecies is said to have a larger and sharper caudal spot.

Postglacial Dispersal

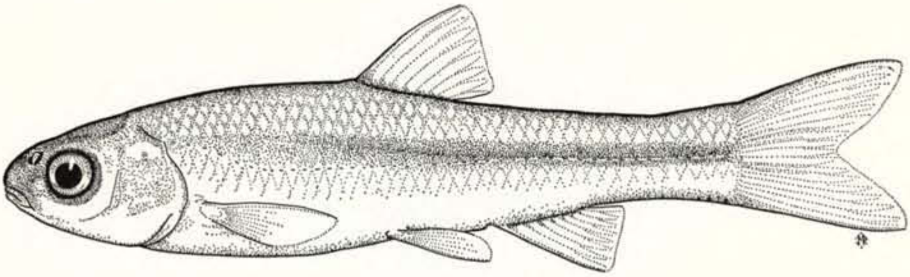
The range of the spottail shiner includes two possible glacial refuges, the Mississippi and Atlantic. The populations now inhabiting the Atlantic coastal plain are perhaps subspecifically distinct (Hubbs and Lagler, 1958) and suggest that *N. hudsonius* survived glaciation in both the Atlantic and Mississippi refuges. In the Mississippi refuge *N. hudsonius* is widely distributed in the upper Mississippi system but apparently absent from the upper Missouri system. This suggests that *N. hudsonius* did not survive glaciation in the Missouri portion of the Mississippi refuge. The populations in our area were probably derived from the upper Mississippi system by postglacial dispersal through Lake Agassiz.

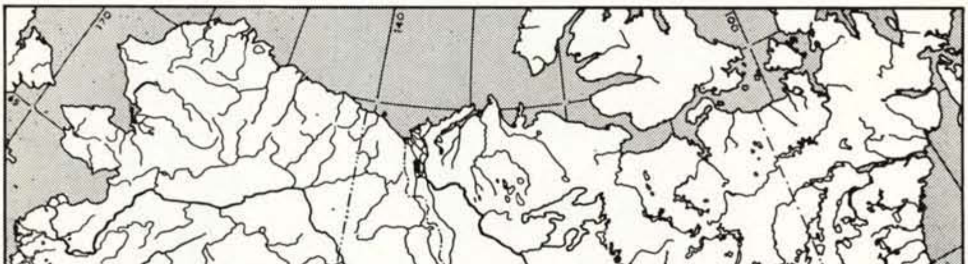
Biology

The spottail shiner is the most northerly ranging species of the large North American genus *Notropis*. It is abundant in the shallows of some large clear northern lakes, including Great Slave Lake. In the north some fish have also been taken from large rather turbid rivers. Bailey and Harrison (1945) report that in Clear Lake, Iowa, both young and adults remain in deeper water during daylight and move inshore at night. Fish from our area contained primarily insect larvae, with some masses of filamentous algae. Plankton, and even small fish, are also reported as food.

Spawning has not been observed in our area, although fish taken from Calling Lake, Alberta, on June 6 had large testes or very large ovaries, and in Nemeiben Lake (Churchill River drainage, Saskatchewan) spawning occurred over sandy shoals on July 10–11 (Peer, 1966).

Elsewhere spawning is said to occur in late June and early July over sandy lake shoals or creek mouths, with no nest construction or parental care. In Nemeiben Lake spawning fish were age III or older; sexual maturity occurs after a total length of approximately 68 mm is reached; the oldest specimens had four annuli.




HYBOGNATHUS
HANKINSONI
0 MILES 400
0 KILOMETRES 600

BRASSY MINNOW

Hybognathus hankinsoni Hubbs

Hybognathus means *protuberant jaw* and *hankinsoni* is named after Dr T. L. Hankinson of Michigan. The French common name for this species is *méné laiton.*

Distinguishing Characters

The large scales, the absence of a barbel, and the origin of the dorsal fin in front of the origin of the pelvic fins.

Description

Body elongate, slightly compressed posteriorly; head short to moderate, about one-third to one-quarter of standard length; eye moderate to large. Mouth small, slightly oblique, jaws sharp-edged; no barbel; pharyngeal teeth 4–4. Branchiostegals 3 + 3; gill rakers moderate, a total of 8–10. Dorsal fin rounded, originates slightly ahead of the origin of the pelvic fins; 8 major dorsal rays; 7–9 major anal rays (usually 8 in our area); 14–16 pectoral rays; and 8 pelvic rays. Pelvic axillary process present. Scales large, cycloid; 36–40 pored scales in the lateral line, which is complete and slightly decurved anteriorly. Vertebrae 36–39 (including the 4 elements of the Weberian region), usually 37 or 38 in our area. Intestines long, much looped; peritoneum jet black.

Size: To 102 mm (4 inches), but usually less than 76 mm (3 inches) in our area.

Sexual dimorphism: The pectorals reach about halfway back to the pelvic origin in females, but well past this point in males.

Colour: Olive-greenish above, paler beneath. The sides have a gold or brassy hue. Sexual changes are said to be slight in this genus; unlike some minnows, males of these fish do not display distinctive red or black pigment in spring. Breeding males reported in Kansas to have tubercles on rays 2–8 of pectoral fins.

Distribution

On the Pacific slope, in several lakes and sloughs in the lower Fraser River valley, and in the upper Fraser River system in the vicinity of Prince George. Also in a restricted region of the upper Peace River system in British Columbia, and in small lakes and ponds (including Taginchil Lake) in an esker complex without external surface drainage, lying about 25 miles northwest of Prince George. The principal distribution lies from southeastern Alberta (Missouri River drainages) east through Saskatchewan and Manitoba to the Ottawa River in Quebec, south to the upper Hudson River, and west to Kansas and Colorado. In our area, recorded only in British Columbia from tributaries to the Parsnip River between Summit and Hart lakes.

Taxonomic Notes

The original description of the brassy minnow as *Hybognathus hankinsoni* appeared in 1929 in Jordan's *Manual of the Vertebrate Animals of the Northeastern United States.* The description was attributed to Dr C. L. Hubbs, who assisted Jordan with the last (13th) edition of the manual. Bailey (1954) designated as the type a specimen from Dead River, Michigan. No subspecies nor name changes have been proposed.

Postglacial Dispersal

The central and eastern areas now occupied by *H. hankinsoni* have probably been populated, since glacial retreat, from a refuge in the Missouri or upper Mississippi systems (Bailey, 1954; Metcalfe, 1966), or both. The species has been found in fossil form in beds of Illinoian age in southwestern Kansas, somewhat south of its present range (Smith, 1963).

A great puzzle is posed by the discovery that, in addition to its distribution in the region discussed, this little minnow also occurs in British Columbia. It is now known from the lower Fraser Valley, the upper Fraser River, and the nearby headwaters of the Mackenzie system, and in the same vicinity was discovered by J. C. Lyons in small lakes without surface outlets.

Artificial introduction by man does not offer a plausible explanation for these western records. Transport and use of live bait fish in British Columbia are not only illegal but are also seldom practiced. Had bait fishermen transported this fish live to its present western sites, they could have obtained no fish from closer than the Missouri River headwaters. Minnows planted in the lower Fraser Valley would have been unable to spread upstream beyond Hell's Gate in the Fraser Canyon. Minnows planted in the upper Fraser River would have had no natural means of access either to the upper Mackenzie system nor to the tiny and remote ponds without drainage in which they have been discovered recently. That each of these disjunct populations has resulted from a separate planting by man is improbable in the extreme. Some of the lakes concerned are small, unattractive, unfished, and could not be reached except on foot until shortly before we collected the species in them.

A clue to the possible source of these populations lies in the glacial geology of the Prince George region. As indicated in the introductory discussion on geology, the upper Fraser system was at one time during glacial recession occupied by large lakes. Apparently the present course of the middle Fraser River was blocked by local ice tongues, and so the lakes in the Prince George and Nechako areas drained north and east towards the present Peace River (Fig. 3). The detailed chronology of the drainage outlets is unknown, but the area northwest of Prince George, within which lie the small lakes in question, was probably traversed by these outlets. Saxton Lake and its tributaries (now draining into the Fraser), and the lakes without drainage (including Taginchil) that lie scattered amongst eskers in the vicinity, all lie in a braided depression that once contained water draining northward from the broad lakes covering the Nechako plain into the valley of the Parsnip River (Armstrong and Tipper, 1948). Our hypothesis is that these waters contained brassy minnows, whose descendents now live in adjacent waters on either side of the Continental Divide, as well as in isolated ponds in the area. They also successfully completed the 400-mile trip downstream through the inimicable Fraser Canyon to become established in suitable waters of the lower Fraser Valley.

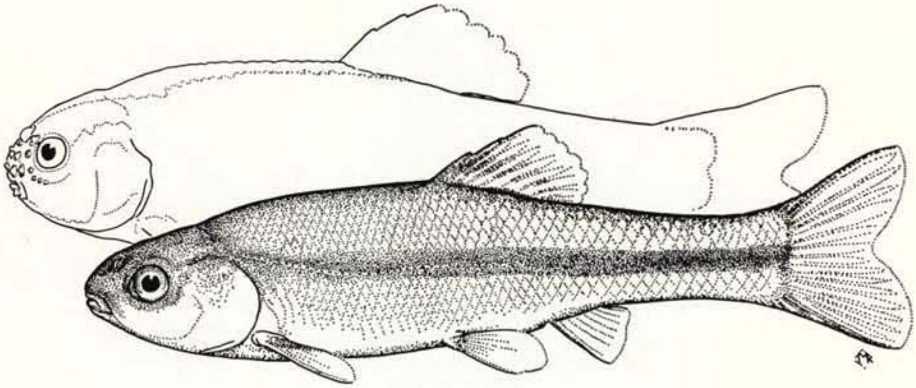
There remains to be explained how the species reached the upper Peace River system from the Missouri. It is known that an extensive lake at one time occupied the Peace River (Fig. 3) and this probably drained southeast (Taylor, 1960). Peace Lake may have received the outflow from the Prince George area. The sequence of the formation of these temporary lakes, and their temporary outlets, is not yet known. But it seems plausible from existing geological evidence that a water connection may have existed east of the Rocky Mountains whereby fish could move north from the Missouri system into waters at that time draining eastward from the Prince George region. If this is the path whereby brassy minnows entered British Columbia, it may be predicted that they will be discovered in some additional Alberta or Saskatchewan waters that lie along the supposed dispersal route. We have in fact devoted some time to searching unsuccessfully in western Alberta for such relict populations. Their present scarcity or absence may be due to the warm postglacial "hypsithermal" period that eliminated fish in marginal habitats, or possibly to subsequent invasion by predatory or competitor species. Alternatively, the dispersal route may have lain farther north, possibly crossing the present Churchill River headwaters, where relict brassy minnows may yet be discovered.

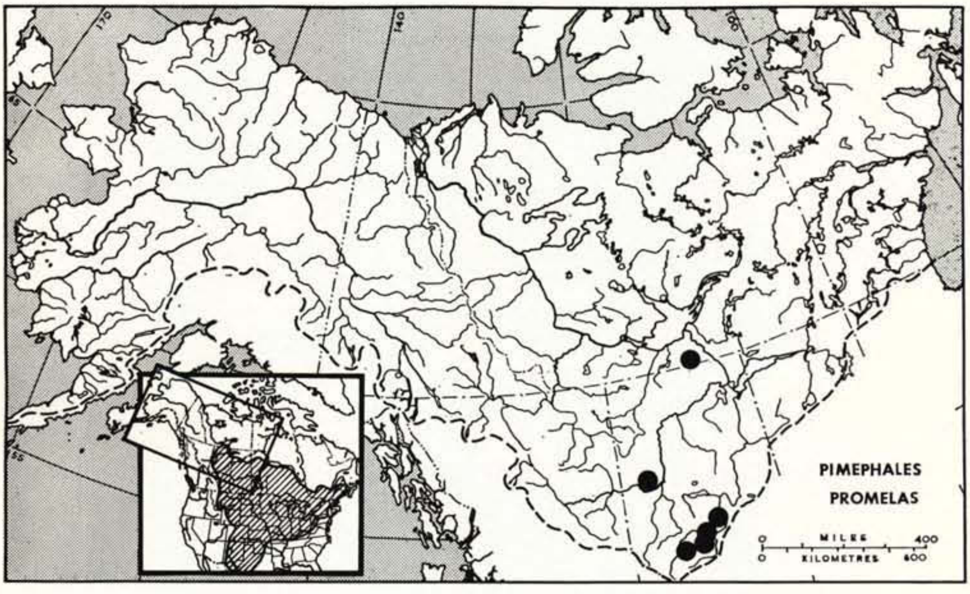
Biology

Brassy minnows in our area have been taken in slow streams, boggy lakes, and shallow bays. In the lower Fraser River, as well as in the east, the species is sometimes common in overflow ponds adjacent to rivers. In the eastern part of its range it is said to prefer stained and acid waters. In Kansas it occupies small clear streams having sluggish current and sandy bottom overlain by organic sediment (Cross, 1967).

Stomachs of fish from the Peace River area contained algae (various filamentous types, and masses of *Chlorococcales*), along with scattered diatoms, ostracods, and a few insect parts. The long looped intestine and jet black peritoneum are commonly found in species with a primarily vegetarian diet. Probably brassy minnows browse on algae and with it ingest associated invertebrates.

Spawning habits have not been recorded. Populations exist in ponds in the Prince George area that have no inlet or outlet streams, so reproduction must be possible in the absence of running water. But females taken in a small stream tributary to Summit Lake in the Peace River drainage on June 16 contained yellow eggs nearly ripe. Females taken elsewhere in the region on June 28 still contained some large eggs, and had evidently not completed spawning for the year. In Kansas reproduction probably occurs in May.




PIMEPHALES
PROMELAS
MILES
KILOMETRES
0
400
0
600

FATHEAD MINNOW

Pimephales promelas Rafinesque

Pimephales means *fathead* and *promelas* means *black before*. The French common name for this species is *tête-de-boule.*

Distinguishing Characters

The blunt head, small mouth without a barbel, moderate-sized scales, and incomplete lateral line. Breeding males have large tubercles on the head.

Description

Body robust, somewhat compressed; head rounded, about one-quarter or more of standard length; eye small, less than snout. Mouth small, never reaching anterior margin of eye, oblique, snout seldom protruding beyond mouth; no barbel; pharyngeal teeth 4–4, one on each side hooked, the rest with oblique grinding surfaces. Branchiostegals 3 + 3; gill rakers short, a total of 12–15. Dorsal fin rounded, originating above origin of pelvic fins; 8 or 9 major dorsal rays; the first obvious ray thickened and separated from the next ray rather than closely attached to it as in most local cyprinids; 7 or 8 major anal rays; 14–18 pectoral rays; and 8 or 9 pelvic rays. Pelvic axillary process poorly developed or absent. Scales moderate, cycloid, 39–51 (usually 40–47 in our area) along the midlateral line; lateral line variable, usually incomplete, 11–38 pored scales. Vertebrae 36–39 (including the 4 elements of the Weberian region). Intestine long, with several loops crossing ventral midline; peritoneum dark to jet black.

Size: To 89 mm (3.5 inches), but usually smaller.

Sexual dimorphism: Breeding males develop large tubercles on the snout and lower jaw, and fine tubercles on the head and pectoral fins. Membranes enveloping the anterior rays of the dorsal fin are thickened, and a spongy predorsal pad forms. These developments are absent in females and nonbreeding males. There is also marked sexual dimorphism in colour.

Colour: Adults are dark olive above and pale below. There is a well-developed dark midlateral stripe that does not extend onto the head. The caudal, anal, and pelvic fins are immaculate (yellowish in life). In females and young the dorsal and pectoral fins are also usually immaculate. In males (particularly during breeding season) the dorsal rays become dark, and the dorsal surface of the first pectoral rays is also darker. In nonbreeding males there is usually a distinct dark spot on the dorsal fin behind the enlarged first ray. In breeding males the head becomes dark except for a light patch on the cheeks and light tubercles. The back also darkens in breeding males, but the distinct vertical lateral banding reported for eastern populations (Trautman, 1957) is not apparent in our area. The young are similar in colour to adults, except that all fins are immaculate.

Distribution

From southern drainages of Great Slave Lake, east to New Brunswick, south to Tennessee, and southern Chihwahua in Mexico. In our area in tributaries to the Peace and Athabasca rivers, only in northern Alberta, and barely extending into the Northwest Territories (Hole Lakes).

Taxonomic Notes

The fathead minnow was originally named from Kentucky as *Pimephales promelas* by Rafinesque in 1820. Synonyms have included *Cliola smithii* and *Hyborhynchus confertus.* Hubbs and Lagler (1964) recognize several subspecies of *Pimephales promelas* including some in Mexico, whereas Bailey (1956) believes that because their variation is clinal the different geographic forms should not be named as separate subspecies. Vandermeer (1966) analyzed geographic variation in eight characters, and also concludes that subspecies should not be recognized. Metcalfe (1966) suggests that present variation may have arisen by partial mixing of stocks isolated in two or three preglacial drainages south of the ice and east of the Continental Divide. If subspecies be recognized, the one in our area is *Pimephales promelas promelas* Rafinesque.

Postglacial Dispersal

The range of the fathead minnow includes the Mississippi glacial refuge, and is widely distributed throughout the upper Mississippi and Missouri systems. Because of the timing and pattern of deglaciation (see "Outline of Geological History") the populations in our area were probably derived from the Missouri system.

Biology

In the northern part of its range this small minnow has been taken in muddy streams and in mud-bottomed lakes. The very long intestine, and pharyngeal teeth with grinding surfaces, are in keeping with the diet of the species. The stomach contents are commonly mud, with sand particles, organic detritus, and microscopic plants and animals. Some northern Albertan specimens had eaten chironomid larvae and quantities of zooplankton.

Spawning, said to occur elsewhere from April to mid-August, has not been observed in our area; females from the Saskatchewan River drainage near Red Deer, Alberta, taken in early August, still contained some large eggs. In the east, eggs are said to be deposited under lily pads or boards, or in excavations under stones, on either horizontal or vertical surfaces, and are guarded by one male. One female may lay eggs in more than one nest, and the spawning period is prolonged. The males, which tend the eggs after fertilization, grow faster than the females and reach a larger size. This is in contrast to many species not showing parental care (e.g., the lake chub, and several species of suckers) in which females reach a larger size than males. In the south some fry hatched in May are said to spawn the same autumn. Cross (1967) believes the fathead minnow is adaptable to erratically fluctuating habitats, but has limited competitive tolerance of other species (each of which may be better equipped to utilize one persistent niche within a stable environment). It is tolerant of a high degree of pollution and oxygen depletion; it occurs abundantly in slow prairie streams of southern Alberta, but is sparse in the wooded southern portion of our area.

THE SUCKERS — Family CATOSTOMIDAE

The suckers are bottom-dwelling fishes with protrusible sucking mouths and fleshy lips, cycloid scales, a single soft dorsal fin, and no adipose fin. Their first four vertebrae are modified into the Weberian apparatus described under the preceding family. The gasbladder has either two or three chambers (two in all species in our area). Their principal difference from the minnows is in the pharyngeal teeth on the last gill arch; most suckers have a single comblike row of many fine teeth (20 or more in our area), apparently used for straining food. Suckers inhabit either lakes or rivers, but seldom enter the sea. Spawning occurs in spring; the species in our area shed large numbers of small adhesive eggs in running water, with no nest construction. Breeding males develop horny rasping protuberances on the anal fin and elsewhere. The young have terminal mouths and feed at first on plankton; later the mouth migrates to the lower surface of the head, and the animals then feed on bottom organisms.

There are about 70 species of suckers, all but 2 of which are found only in North America. A relict form living in the Yangtse drainage in China, and fossil suckers in both Asia and North America, leave the question open as to which continent was the original home of the group. Whether suckers gave rise to minnows, or vice versa, is also uncertain. In our area only three species occur, all in the genus *Catostomus*.

KEY TO THE SPECIES

1(8) Lower lip with two sides separated into two conspicuous lobes by a median cleft 2

2(3) Distinct notch at each corner of mouth between upper and lower lips; median cleft in lower lip shallow, with 3–5 rows of papillae crossing ahead of its base ....
.... Mountain sucker, *Catostomus platyrhynchus* (Cope)
Not recorded from our area but known from the Fraser and Saskatchewan river systems. Formerly placed in the genus *Pantosteus*, and including the species *jordani*.

3(2) No notches at corners of mouth; median cleft in lower lip deep, usually with no papillae (and never more than 2 rows) crossing ahead of its base 4

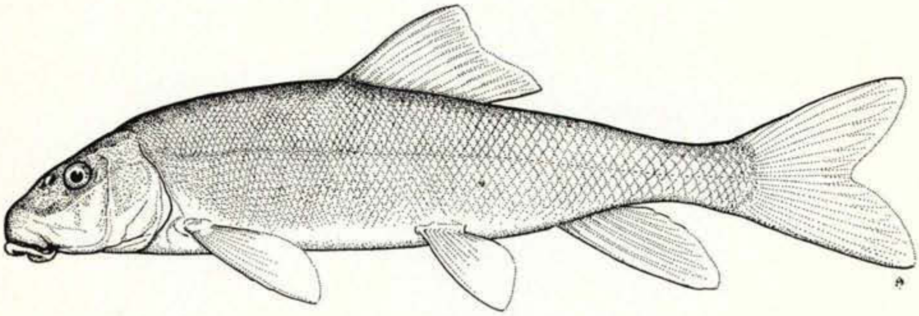
4(7) Scales large, 16–21 horizontal rows around caudal peduncle 5

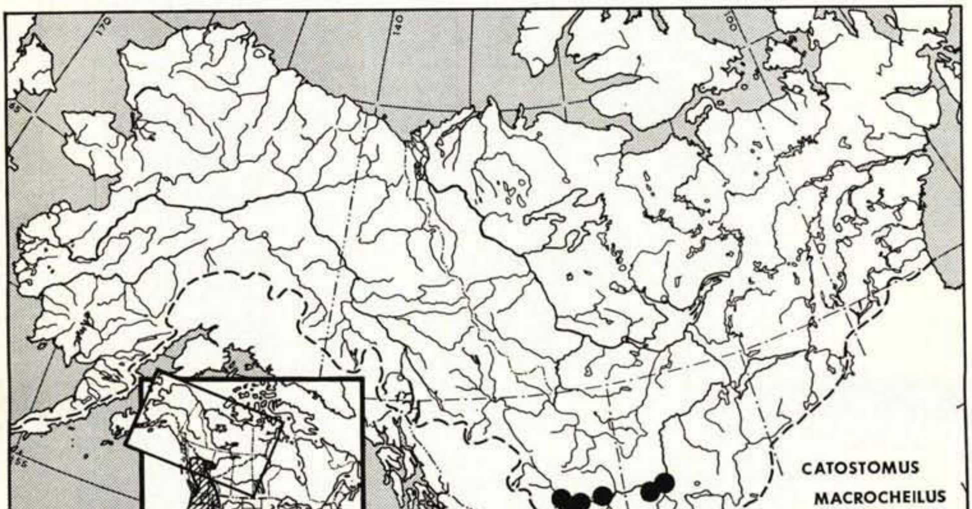
5(6) Caudal peduncle narrow, its depth less than half the dorsal fin base, except in very big fish (over 15 inches long); gill rakers 25–37 (usually more than 26) ....
.... Largescale sucker, *Catostomus macrocheilus* Girard (p. 277)

6(5) Caudal peduncle deeper, its depth more than half the dorsal fin base; gill rakers 20–27 (usually less than 26) ....
.... White sucker, *Catostomus commersoni* (Lacépède) (p. 281)

7(4) Scales small, 26–34 horizontal rows around caudal peduncle ....
...... Longnose sucker, *Catostomus catostomus* (Forster) (p. 285)

8(1) Lower lip not separated into two conspicuous lobes, its posterior margin without a distinct median cleft ....
.... Northern redhorse, *Moxostoma macrolepidotum* (LeSueur)
A deep-bodied sucker with a three-chambered gasbladder, not recorded from our area but known from the Saskatchewan River system.




CATOSTOMUS
MACROCHEILUS
MILES
0
400
KILOMETRES
0
600

LARGESCALE SUCKER

Catostomus macrocheilus Girard

Catostomus means *inferior mouth* (beneath the snout) and *macrocheilus* means *large lip*. The French common name for this species is *meunier à grandes écailles*.

Distinguishing Characters

The ventral sucking mouth with large lips, the single dorsal fin with 12–16 rays, the large scales, and narrow caudal peduncle.

Description

Body elongate, tapering rapidly behind the dorsal fin; head moderate, usually less than one-quarter standard length; snout blunt, about 2.5 times horizontal eye diameter. Mouth ventral, the lips large and with coarse papillae. Distance from dorsal fin origin to pelvic fin origin more than 2.5 times the least caudal peduncle height (except in some large fish, over 30 cm fork length). Branchiostegals 3 + 3; gill rakers short and fleshy, 25–37; pharyngeal teeth in a single row, comblike, 43–46 + 43–48 (five specimens). Dorsal fin large, with 12–17 major rays (usually 13–15); 7 major anal rays; 16–18 pectoral rays; and 10 or 11 pelvic rays. Scales large, cycloid, 62–83 pored scales in lateral line, 11–15 scales in diagonal row from dorsal fin (anterior to the first rudimentary ray) downward and backward to but not including the lateral line. Vertebrae (including the Weberian region) 47–49; stomach scarcely differentiated from gut, no pyloric caeca; peritoneum usually dark.

Size: Length to 61 cm (24 inches, usually less than 20 inches), weight to 3.2 kg (7 lb).

Sexual dimorphism: No obvious external differences between sexes except at spawning time. Breeding males with well-developed horny white tubercles on anal fin and lower caudal fin. These are absent or weakly developed in females. Most spawning females are larger than most spawning males. The lateral band is blacker, and the bicoloured pattern more striking in spawning males than in females.

Colour: In adults the back and sides are bluish grey to olive; the sides and underparts are white or yellow–white. A dark lateral band extends from the snout to the caudal peduncle below the lateral line. Fins usually immaculate except for a dark leading edge on dorsal fin, sometimes with a white leading edge with dark behind it. Young (up to 6 inches) sometimes have three or four diffuse dark blotches on sides.

Distribution

On the Pacific slope from the Nass River south to Sixes River, Oregon, and east of the Continental Divide in the upper Peace River downstream to the junction of Smoky River in Alberta.

Taxonomic Notes

The largescale sucker was originally named from Oregon as *Catostomus macrocheilus* by Girard in 1856. *Catostomus tsiltcoosensis* is the only synonym. The species is of Pacific slope origin, and is distinct from the white sucker *Catostomus commersoni*, which is a large-scaled counterpart widespread east of the Continental Divide. In four lakes of the upper Peace River system (Tudyah, McLeod, Kerry, and Summit) hybrids have been found between *Catostomus commersoni* and *Catostomus macrocheilus.* According to Nelson (1968a), such hybrids form about 7% of the populations examined there and in lakes of the upper Fraser River system. Although no complete barrier to interbreeding has evolved, either the amount of hybridization or the survival of hybrids must be low, for even in lakes where hybrids occur the great majority of individuals are apparently pure forms of one or the other species. Hybrids may be recognized by their intermediacy in all the morphological characters that distinguish the parental species (Nelson, 1968a).

Postglacial Dispersal

The range of the largescale sucker includes only one possible glacial refuge, the Pacific. The populations in our area attained their present distribution by postglacial dispersal northwards from the Columbia system into the Fraser River, and from the Fraser system eastward across the Continental Divide into the upper Peace River (Mackenzie system).

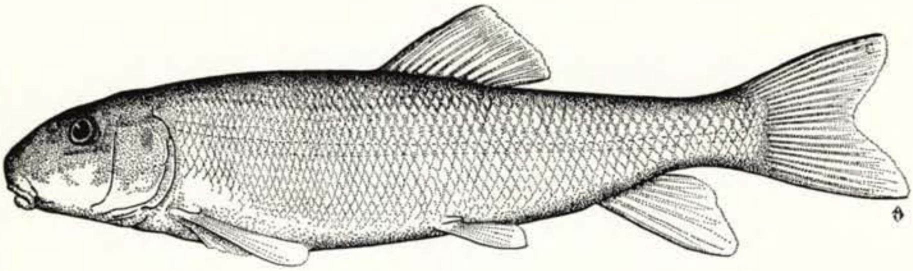
Biology

The largescale sucker occupies lakes and large rivers. It remains close to the bottom day and night at depths usually of a few feet but occasionally up to at least 27 m (80 ft), feeding on crustaceans, insect larvae, molluscs, and other organisms associated with the bottom. Quantities of unidentifiable detritus are usually present. This species probably reaches sexual maturity after about 5 years in males and 6 years in females. Clemens et al. (1939) report that a Woods Lake (Okanagan) specimen 540 mm (21.2 inches) long was about 15 years old.

Spawning occurs commonly in lake outlets, but sometimes in inlet streams and occasionally along lake margins. Largescale suckers seem to prefer deeper sand-bottomed areas for spawning (Nelson, 1968a). In central British Columbia spawning extends from mid-May to late June, although it may be as early as late April in the lower Fraser Valley. Where they occupy the same lake, largescale suckers spawn a week or more later than longnose suckers; the spawning period of the white sucker overlaps that of the largescale although the latter on the average spawns slightly later. The eggs, which are yellow and adhesive when laid, hatch in about 2 weeks.

Studies at Nicola Lake in southern British Columbia (T. Miura, personal communication) showed that in early summer the young fry of this species swam in schools in midwater or near the surface, feeding on pelagic crustaceans; by late summer they had taken to feeding on small bottom organisms. These changes are associated with a gradual migration of the mouth from a terminal to a ventral position. Fry moved inshore into very shallow water to feed during daylight hours, and off into somewhat deeper water at night.

The flesh is edible, although bony, and may sometimes be sold incognito in fish-and-chip emporia.




CATOSTOMUS
COMMERSONI
MILES
0
400
KILOMETRES
0
600

WHITE SUCKER

Catostomus commersoni (Lacépède)

Commersoni is named after P. Commerson, an early French naturalist. The French common name for this species is *meunier noir*.

Distinguishing Characters

The ventral sucking mouth with large lips, the single dorsal fin with 10–13 rays, the large scales, and thick caudal peduncle.

Description

Body elongate, almost round in cross-section; head moderate, about one-quarter standard length; snout blunt, about 4 times horizontal eye diameter. Mouth ventral, without teeth; lips large with coarse papillae. Distance from dorsal fin origin to pelvic fin origin less than 2.5 times the least caudal peduncle height (except in some large fish, over 30 cm fork length). Branchiostegals 3 + 3; gill rakers short and fleshy, 20–27; pharyngeal teeth in a single row, comblike, 40–42 + 39–43 (five specimens). Dorsal fin with 10–12 (or rarely 13) major rays; 7 or 8 major anal rays; 16–18 pectoral rays; and 10 or 11 pelvic rays. Scales large, cycloid, 60–74 pored scales in the lateral line, 9–11 scales in diagonal row from dorsal fin (anterior to the first rudimentary ray), downward and backward to, but not including, the lateral line. Vertebrae 45–48 (including the Weberian region); stomach scarcely differentiated from gut, no pyloric caeca; peritoneum pale or speckled.

Size: Length to 635 mm (25 inches) (usually less than 20 inches), and weight to 3.2 kg (7 lb).

Sexual dimorphism: No obvious external differences between sexes except at spawning time. Breeding males have well-developed tubercles on the anal and caudal fins, and on some scales. In breeding females these tubercles are either absent or reduced in size and number. In spawning populations most females are usually larger than most males. The dark and light pattern of the sides is more pronounced in males.

Colour: Adults with brassy brown to black backs, silvery white sides and underparts, and a dark stripe just below the lateral line. Fins usually immaculate, pectoral fin often with a white leading edge. Young (up to 6 inches) usually with three dark blotches on sides and a dark blotch showing through the operculum. A rosy lateral stripe has been reported in spawning males in the eastern range of this species, but we have observed no red in any specimens from our area, even in live spawners from the upper Peace River system.

Distribution

From the Mackenzie River east to Labrador and Nova Scotia, south to Georgia, Oklahoma, and New Mexico. Introduced into the Colorado River system. On the Pacific slope, in the Skeena River, and also in several lakes of the upper Fraser system, as far south as Green Lake in central British Columbia. In our area, throughout most of the Mackenzie River system, from Great Slave Lake south, and in the mainstem north to Good Hope and possibly to Arctic Red River (Walters, 1955), but not taken in Great Bear Lake. Apparently absent from the Barren Grounds, but present in Wholdaia and perhaps in Nueltin Lakes (Fowler, 1948).

Taxonomic Notes

The white sucker was originally described as *Cyprinus commersonnii* by Lacépède in 1803, from a specimen of unknown origin. Many specific names have been applied, including *teres, communis, flexuosus, reticulatus, gracilis, pallidus,* and *chloropteron.* A poorly differentiated Great Plains form, *Catostomus commersoni suckleyi,* is thought by Bailey and Allum (1962) not to warrant subspecific separation from the eastern form. A dwarf form in the Adirondacks that spawns late has been referred to as *Catostomus commersoni utawana.* Three geographically separated forms may have occupied the eastern, the Ancestral Plains Stream, and Hudson Bay drainages respectively, distinguished by body thickness, eye size, scale count, and number of lip papillae (Metcalfe, 1966). Also, eastern populations are said to produce red-banded spawning males, whereas we have seen no colour in fish from our area nor from the Fraser River system. "Assuming that such distinctiveness did exist, it has been blurred subsequently in the Mississippi River system by Pleistocene mingling of stocks caused by advances of glacial ice, compression of ranges and changes in stream connections" (Metcalfe, 1966).

Hybridization with the western species *Catostomus macrocheilus* in lakes of the upper Peace and upper Fraser river systems (Nelson, 1968a) has been described under the latter species. Hybrids, which are recognizable by their morphological intermediacy, may be expected to occur farther down the Mackenzie River system if *C. macrocheilus* is still extending its range into the territory of *C. commersoni.*

Postglacial Dispersal

The wide range of *C. commersoni* includes two possible Wisconsin glacial refuges, the Mississippi and the Atlantic. The white sucker probably survived glaciation in both areas; the populations in our region were almost certainly derived from the Mississippi refuge. Because of the timing and direction of deglaciation on the Great Plains, white suckers in our area are probably derived primarily from the upper Missouri system.

The rather widespread distribution of white suckers in the upper Fraser, Skeena, and upper Peace systems suggests either an early postglacial entry into British

Columbia via the Peace River region, or conceivably the persistence throughout Wisconsin glaciation of a refuge in glacial Lake Peace in Alberta, or even in the Prince George region. A search for small differences across the present range of the white sucker may reveal evidence as to how many separated populations persisted during glaciation.

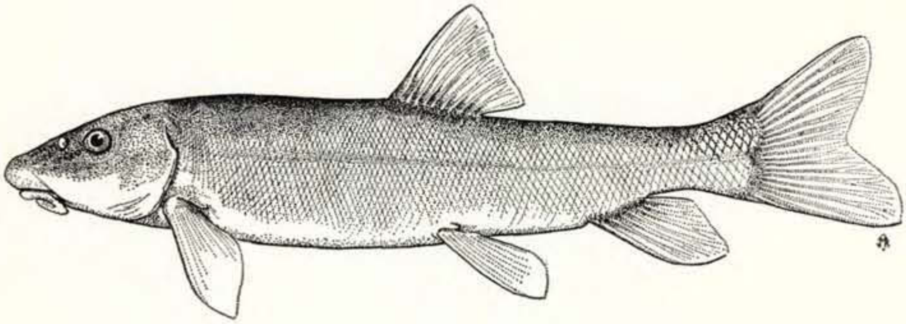
Biology

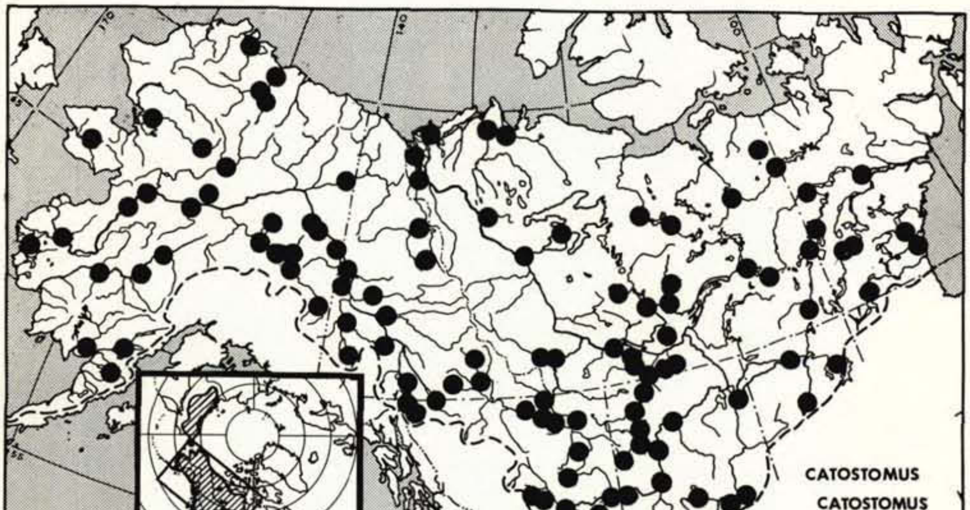
In the south, the white sucker is tolerant of a wide variety of lake and stream conditions, but towards the northern limit of its range in our area it is restricted to the warmer shallows. Although it has been taken from the Mackenzie River as far north as the Arctic Circle, it is apparently absent from the Great Bear Lake, and in Great Slave Lake it it almost limited to Yellowknife Bay and the north arm near Fort Rae. Even in Lake Athabasca it is restricted to a limited area of shallow water, but in upper Peace River drainages it is widespread and abundant.

The adults are strictly bottom feeders. Rawson (1951) found Great Slave Lake fish feeding about one-third on midge larvae, and one-third on amphipods, with lesser quantities of molluscs and caddis larvae. The young fry probably feed on plankton, but as they grow they turn more and more to the larger bottom organisms. Sexual maturity is reached in 5–7 years. Great Slave Lake fish reached a fork length of 51 cm (20 inches) at age 10; the oldest recorded there was 12 years old (Rawson, 1951).

White suckers spawn in inlet or outlet streams or along lake margins, in the Peace River area from mid-May to early June, often in the same areas as, but later than, the longnose sucker. White suckers favour shallow gravel areas for spawning (Nelson, 1968a). In a central British Columbia lake the onset of the spawning run into the inlet stream was not related to stream flow but occurred each year when stream temperatures first exceeded 10 C (50 F) (Geen et al., 1966). Several males may cluster alongside one larger female during the spawning act, probably pressing her with their tubercle-covered fins. Sperm and yellowish adhesive eggs are shed simultaneously. A female may contain over 50,000 eggs. Hatching occurs in about 8 days at 11 C; fry may remain in the gravel 1–2 weeks before emerging. Many white suckers survive to spawn in several successive years; in Sixteenmile Lake, B.C., 1.8% of the spawners in 1962 had been marked in the 1956 spawning run (Geen et al., 1966).

The flesh of the white sucker is good to eat, particularly if taken from cold water. It has been canned successfully. Suckers, called "carp" by the fur traders, were sometimes an important food. Early journals describe the visits of Indians from Fort McLeod on the Parsnip River drainage to net fish from Carp Lake, where white suckers still abound. Sir John Richardson wrote that the "grey-sucking-carp" was considered to be one of the best in the country for making soup. He adds this bit of lore: "The brain is protected by a piece of cartilage which, on maceration or boiling, drops out, leaving a rectangular opening before the nape one inch long and a quarter of an inch wide. When the head is cooled the brain becomes visible through this opening, and is supposed, by the Indians, to be a small frog, which resides within the head of the fish."




CATOSTOMUS
CATOSTOMUS
0 MILES 400
0 KILOMETRES 600

LONGNOSE SUCKER

Catostomus catostomus (Forster)

Catostomus means *inferior mouth* (beneath the snout). The French common name for this species is *meunier rouge.*

Distinguishing Characters

The ventral sucking mouth with large lips, the single soft dorsal with 9–11 rays, the small scales, and long snout. Any sucker taken in Alaska or the Yukon River system is probably this species.

Description

Body elongate, almost round in cross-section; head moderate, usually less than one-quarter standard length; snout somewhat pointed, about 3–5 times horizontal eye diameter. Mouth ventral, without teeth; lips large and with coarse papillae. Branchiostegals 3 + 3; gill rakers short and fleshy, 23–30; pharyngeal teeth in a single row, comblike, 37–45 + 35–46 (K. Sandercock, 15 specimens). Dorsal fin with 9–11 major rays; 7 major anal rays; 16–18 pectoral rays; and 10 or 11 pelvic rays. Scales small, cycloid, crowded towards the head, 90–120 pored scales in the lateral line. Vertebrae 45–47 (including the Weberian region); stomach scarcely differentiated from gut, no pyloric caeca; peritoneum silvery to jet black, varying from river system to river system.

Size: Length to 635 mm (25 inches) (usually much less) and weight to 3.2 kg (7 lb).

Sexual dimorphism: No obvious external differences except at spawning time. Breeding males have well-developed tubercles on the head, anal, and caudal fins. These are absent or weakly developed in females. Breeding males are much more vividly coloured than females.

Colour: In adults the back and sides are dark grey to black, underparts white. Breeding males with dark bands along the back and lateral line, separated by a wide brilliant red stripe. Young (to 8 inches) with irregular pale patches on the back.

Distribution

In Siberia, in Arctic Ocean drainages from the Yana to the Kolyma rivers, and in headwaters of the Anadyr River. In North America, widespread from Alaska to Labrador and New Brunswick, south to Pennsylvania and Maryland, the northern margin of the Mississippi River system to Minnesota, and Colorado; west of the Continental Divide in most rivers from the Columbia River north to the Gulf of Alaska. In our area, in almost every mainland drainage system sampled. Not reported from any island of the Bering Sea nor of the Canadian Arctic Archipelago.

Taxonomic Notes

The longnose sucker was originally described from streams about Hudson Bay as *Cyprinus catostomus* by Forster in 1773. Many other species or subspecies have been named that are now considered to be *Catostomus catostomus,* including *retropinnis, griseus, richardsoni,* and *rostratus.* Dwarf, often late-spawning forms have been considered separate subspecies (*nannomyzon* in the east, *pocatello* in Idaho and Montana); similar dwarf late-spawning races occupy Edwards Lake in southwestern British Columbia, and several drainage systems in southwestern British Columbia and western Washington. Some of these diverse forms may warrant subspecific designations, but at present we are too ignorant of the degree to which the differences depend on direct environmental (phenotypic) modification to make reliable subdivisions.

Within our area there appear to be two allopatric morphological forms of *C. catostomus.* The character most useful in separating these two forms is the number of gill rakers. In Bering Sea drainages *C. catostomus* has 23–29 gill rakers (the means are usually about 25 or 26) whereas longnose suckers from the Mackenzie system and rivers to the east have 25–30 gill rakers (the means are usually near 27 or 28). These differences probably resulted from isolation in separate glacial refuges in the Bering and Mississippi regions. Relationships with forms on the Pacific slope south of glaciation are as yet unclear.

Postglacial Dispersal

The present range of the longnose sucker includes three glacial refuges: the Bering, the Mississippi, and the Pacific. There are still relict populations of *C. catostomus* in the Mississippi and Pacific refuges. This indicates the longnose sucker survived glaciation in these areas, and its presence in the Chukotsk area of eastern Siberia indicates it also survived in the Bering refuge. Within our area there are two allopatric morphological forms of *C. catostomus* (see "Taxonomic Notes"). The distribution of these suggests that the longnose sucker has postglacially expanded its range into the glaciated parts of our area from two refuges: the Bering and Mississippi. In our area the Bering form is confined to Alaska (the populations in Siberia appear to be identical). The Mississippi form has a wider range in our area and is found in the Mackenzie system and many lakes and rivers on the Barren Grounds.

Biology

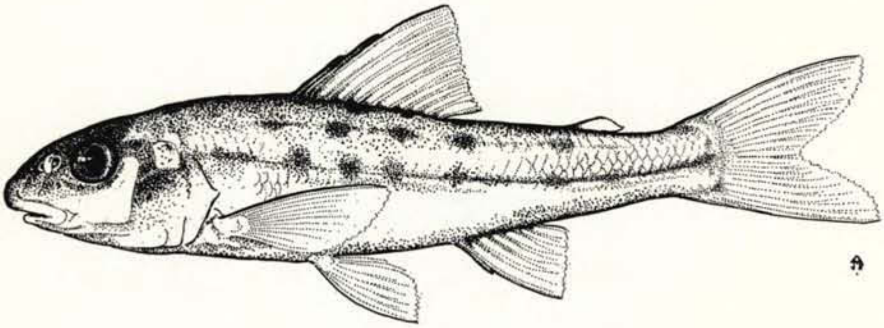
The longnose sucker is the most widespread and successful of the northern cypriniforms (minnows and suckers). It is ubiquitous in the mainland drainages of our area, and is the only cypriniform species that exists in Siberia as well as North America. Unlike most other cypriniforms, in the arctic it is "abundant at times in brackish water around river mouths" (Walters, 1955). In Great Bear Lake it is seldom encountered in the lake proper, but is quite common in tributary streams (Miller, 1947). In Great Slave Lake it is much more abundant than the white sucker, and in 1944–45 made up 7% of the commercial summer fishery. It goes down to considerable depths, but in Great Slave Lake is uncommon below 17 m (50 ft). Specimens taken from that lake contained 63% amphipods (mostly *Pontoporeia*), 15% midge larvae, 11% caddis fly larvae, and 9% sphaeriid clams (Rawson, 1951). There it reaches a fork length of 483 mm (19 inches) in about 10 years; the oldest fish studied was aged 14 years. In central British Columbia males first spawn at about 5 years of age, females at 6 or 7; some survive to spawn in several consecutive years.

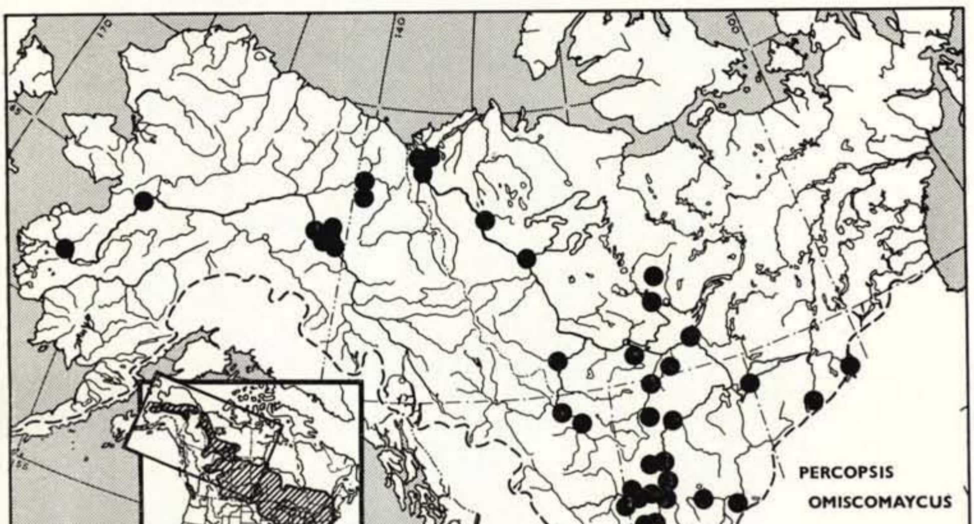
Spawning occurs usually in inlet streams, but can take place in outlets or the shallows of lakes. Breeding usually commences shortly after the melting of ice cover on the lakes, from April to late May in central British Columbia, but presumably later in the arctic. Entry into the inlet stream at Sixteenmile Lake, B.C., commenced when water temperature first exceeded 5 C (41 F) (Geen et al., 1966). In the Kolyma River system in Siberia longnose suckers spawn in June, after the ice flow, in swift sections of gravelly rivers (Nikolsky, 1961). The eggs are whitish and adhesive when shed. Under laboratory conditions eggs hatch in 8 days at 15 C (59 F) and 11 days at 10 C (50 F). Young remain in the gravel 1–2 weeks before emerging.

Hinks (1957) writes that longnose sucker flesh has a better flavour than that of many other suckers, and may be profitably canned in the future. Frozen fillets find a ready market in the Great Lakes under the name of "mullet." In the Yukon River it was a food fish of considerable importance, especially to the Indians (Evermann and Goldsborough, 1907), and throughout the north, including Siberia, longnose sucker meat has been widely eaten as human and dog food. Richardson (1836) says the "red sucking carp" makes a more gelatinous soup than any of the northern fish, and is the best bait for trout or pike.

THE TROUT-PERCHES — Family PERCOPSIDAE

As the name implies, trout-perches combine some characters of the more primitive troutlike fish (notably a small adipose fin, and pelvic fins placed well behind the pectorals) with some characters of the more advanced spiny-rayed fishes (small spines in the fins, rough ctenoid scales, a perchlike mouth). They are small blunt-headed fish, translucent when alive. The family contains only two species, one found only in the Columbia river system, the other more widespread in North America.





170
140
100
155
PERCOPSIS
OMISCOMAYCUS
MILES
400
KILOMETRES
600

TROUT-PERCH

Percopsis omiscomaycus (Walbaum)

Percopsis means *perchlike* and *omiscomaycus* is probably an Algonkian Indian name that includes the root "trout." The French common name for this species is *omisco.*

Distinguishing Characters

The small adipose fin, large rough (ctenoid) scales, and pectoral fins extending well back past the start of the pelvic fins.

Description

Body elongate, tapering posteriorly; head large, more than one-quarter standard length; snout long, about twice eye diameter. Mouth small, overhung by conical snout; numerous fine teeth on the premaxillary and dentary; no teeth on maxillary, tongue, or basibranchials. Branchiostegals 6 + 6; gill rakers short, stubby, bearing small teeth, 2–4 + 6–9. Preopercle often with a single well-developed spine at the angle of a raised crest. Dorsal fin originates anterior to origin of pelvic fins, with 2 spines and 10 or 12 soft rays; anal fin with 1 spine and 6 or 7 soft rays; 12 pectoral rays; 1 pelvic spine, and 8 soft rays. Scales large, ctenoid, 41–54 pored scales in lateral line, nape usually scaleless. Vertebrae 33–36. Pyloric caeca 7–11.

Size: In our area usually to 100 mm (4 inches) but farther south occasionally to 200 mm (about 8 inches).

Sexual dimorphism: There are no obvious external differences between the sexes.

Colour: In adults the back is silvery with a purplish tinge, the sides are partially transparent and the silvery-white peritoneum shows through the body wall. There is usually a row of about 10 small dark blotches along the midlateral line and another row of small dark spots (usually less than 10) between this and the back. There is often a series of dark blotches along the midline of the back.

Distribution

Found only in North America. From West Virginia and the Mississippi, a small portion of the lower Missouri, and the St. Lawrence systems, north to the Mackenzie and Yukon rivers. In our area the trout-perch is found throughout the Mackenzie system from its headwaters to the Mackenzie Delta (except for the upper Liard and upper Peace River), but in the Yukon system it is known only from the Porcupine River and the main-stem Yukon River from about Eagle downstream to the mouth of the Andreafsky River. It has not been taken in the upper Yukon system in the Yukon Territory nor in major southern tributaries such as the Tanana River.

Taxonomic Notes

The trout-perch was originally named as *Salmo omiscomaycus* by Walbaum in 1792, following the description (without a Latin name) of this fish from the Albany River by Thomas Pennant in 1784. It was placed in the genus *Percopsis* by Agassiz in 1848. Other specific names that have been used in the past are *guttatus, pellucida,* and *hammondii.* There appears to be little geographic variation in the trout-perch in our area.

Postglacial Dispersal

The present distribution of the trout-perch encompasses two possible glacial refuges: the upper Mississippi Valley and the lower Yukon River system. As noted above, there is no consistent pattern of geographic variation in this species. In particular, the populations in the Yukon system do not differ morphologically from those in the Mackenzie system nor from those farther south. Hence all of the populations in our area were probably derived postglacially from a single source, probably the upper Mississippi Valley. Absence of the trout-perch from the upper Missouri indicates that it did not enter our area (as many species did) from the upper Missouri system. In addition, the present distribution in the Yukon system (particularly its absence from the Tanana and upper Yukon rivers) suggests that the trout-perch has only recently entered the Yukon system. This entry was probably by way of headwater capture or some other drainage connection between the Peel River (Mackenzie system) and the Porcupine River (Yukon system). The trout-perch is probably still expanding its range in the Yukon system.

Biology

Trout-perch are typically found in quiet backwaters of large, muddy rivers, and along shallow sandy beaches in lakes. In lakes there is often a marked diurnal onshore movement of trout-perch; daytime seining will produce almost no trout-perch, but the same areas at night contain large populations. Magnuson and Smith

(1963) also noted a difference in summer distribution of juveniles and adults in Lower Red Lake, Minnesota. The juveniles remained for the most part in deeper water, whereas the adults concentrated in shallows for spawning. Trout-perch feed mainly on aquatic insects, small crustaceans, and molluscs. The stomachs of 30 specimens from the Muskwa River near Fort Nelson, B.C., all contained aquatic insects. Just before spawning season (early June) in the Muskwa River the smallest size-group present (presumably 1-year-old fish) average about 35 mm (1.5 inches) in total length. The largest fish (females) were all less than 90 mm (3.5 inches). In Minnesota 2-year-old females average 90 mm in length and 3-year-old females average about 105 mm. Growth rate is apparently slower in our area than in southern regions. Nothing is known about age at maturity or maximum age in our area. In Minnesota, Magnuson and Smith indicate that some individuals reach sexual maturity in their 2nd year, and that the maximum age is 4 years.

Spawning occurs in the late spring and early summer. In our area ripe males and females have been taken in the Muskwa River from June 5 to July 21. In the Yukon system ripe specimens were taken at Circle, Alaska, on June 28, 1958. Spawning takes place in slow streams or along lake beaches. Most spawning apparently occurs at night. Magnuson and Smith describe spawning in Mud Creek (a tributary of Lower Red Lake), Minnesota, as occurring within 4 or 5 inches of the surface near the edges of the stream. Several males cluster around and press close to the sides of the female. Eggs and milt are released simultaneously. The eggs are quite small (about 1.5 mm in diameter before fertilization), adhesive, and denser than water. After fertilization they sink to the bottom and stick to whatever they contact. Up to 700 eggs are laid by a single female; they hatch in about 1 week.

Trout-perch are of no direct commercial value, but are important forage fish for lake trout and walleye. In thermally stratified lakes trout-perch may serve as nutrient transporters, feeding at night in the shallows and moving during daylight into deeper water where they are eaten by lake trout that are confined to the cooler depths.

THE CODS — Family GADIDAE

Codfishes have two or three dorsal fins and one or two anal fins, but none of the fins are spiny. The pelvic fins lie ahead of the pectorals. The chin carries a whiskerlike barbel. All but one of the 60-odd species occur in cold or temperate seas, mostly in the northern hemisphere. Marine cods are of immense commercial importance. Only the burbot, *Lota lota,* is adapted to a purely freshwater existence, but three other species in our area frequently enter fresh water and are therefore included in the key.

KEY TO THE SPECIES

1(6) Three dorsal and two anal fins; caudal fin not rounded 2

2(5) Snout projecting beyond mouth; fewer than 30 gill rakers 3

3(4) Barbel almost equal to eye diameter; mouth large, upper jaw usually longer than snout .... Pacific cod, *Gadus macrocephalus* Tilesius

A North Pacific and Bering Sea species that sometimes enters fresh water in the Bristol Bay region of Alaska.

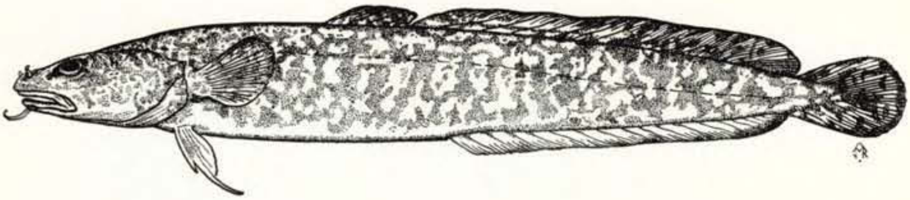
4(3) Barbel about one-half eye diameter; mouth smaller, shorter than snout .... Saffron cod, *Eleginus navaga* (Pallas)

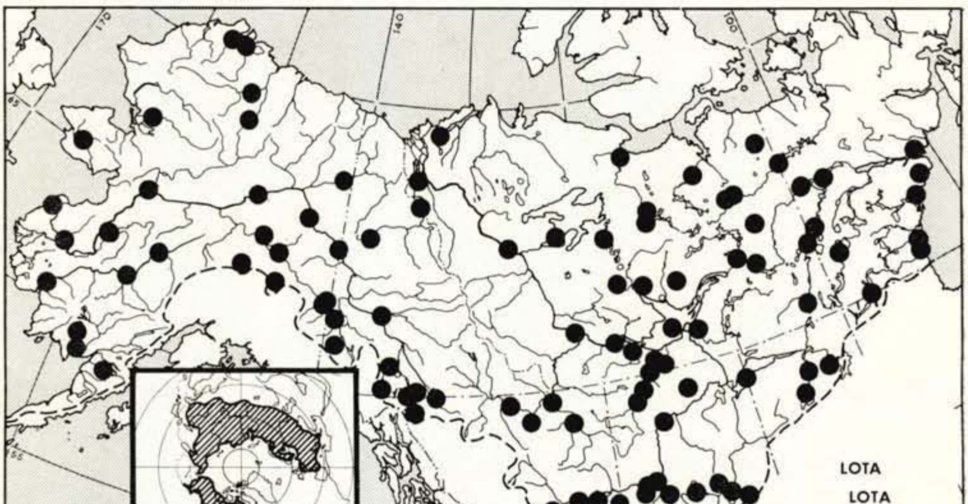
A yellow-sided fish occurring in the Bering Sea and the Arctic Ocean, apparently breeding in the sea but entering the lower sections of rivers.

5(2) Lower jaw projecting beyond mouth; more than 30 gill rakers .... Arctic cod, *Boreogadus saida* (Lepechin)

A circumpolar species that readily stays in the vicinity of ice, and sometimes enters rivers.

6(1) Two dorsal fins and one anal fin; caudal fin rounded .... Burbot, *Lota lota* (Linnaeus) (p. 297)




170
140
100
65
155
LOTA
LOTA
0 MILES 400
0 KILOMETRES 600

BURBOT

Lota lota (Linnaeus)

Lota is from an old French name. The French common name for this species is *lotte.*

Distinguishing Characters

The elongate body tapering to a point posteriorly, and the whiskerlike barbel on the tip of the chin.

Description

Body elongate, tapering to a point posteriorly; head short, flattened, about one-fifth total length; snout long, about 3 times eye diameter. Mouth terminal, large; numerous fine teeth on the premaxillary, dentary, and head of vomer; no teeth on the maxillary, tongue, or basibranchials. Branchiostegals 6–8 + 6–8; gill rakers short, 7–12 on the first arch. First dorsal fin rays 8–16; second dorsal fin rays 60–80; 58–77 anal rays; 17–21 pectoral rays; and 5–8 pelvic rays, the second pelvic ray long and filamentous. Scales extremely small and embedded. Vertebrae 53–66. Pyloric caeca 31–150.

Size: Weight to 34 kg (75 lb) and length to 122 cm (4 ft). The largest Great Slave Lake burbot recorded weighed 8.4 kg (18.5 lb) and was 94 cm (36.9 inches) long; Alaskan burbot may reach 27 kg (60 lb).

Sexual dimorphism: There are no obvious external differences between the sexes.

Colour: The back and sides of adults are olive green to dark brown, with irregular pale blotches; the underparts are usually a pale yellow–white, but occasionally speckled. The pectorals, dorsals, caudal, and anal fins are strongly mottled.

Distribution

Across northern Eurasia from England to Bering Strait, south to northern Italy, the Caspian, and Korea. In North America, on the Pacific slope as far south as the Columbia River (but not below the canyon in the Fraser River), in Bering Sea and Arctic Ocean mainland drainages east to Labrador, south to the Connecticut, Delaware, and Susquehanna river systems, the Great Lakes basin, and in the Mississippi River system south to Missouri. Recorded from most mainland drainages in our area. Enters brackish water, but not taken on islands in our area.

Taxonomic Notes

Linnaeus named the burbot in Europe as *Gadus lota* in 1758. The eastern North American form was later named as a separate species, *Gadus lacustris,* also called *Gadus maculosus.* Hubbs and Schultz (1941) recognized three subspecies, *Lota lota lota* of Europe, *L. l. maculosus* of eastern North America, and *L. l. leptura,* an Alaskan form distinguished by its long narrow caudal peduncle. Lindsey (1956) and Lawler (1962) demonstrated a cline in this character, and suggested that subspecific recognition of the Alaskan form is not warranted. However, comparison of the number of gill rakers and of pyloric caeca in *Lota* also shows that two morphological forms occur in our area. Burbot found in Bering Sea drainages have 8–12 gill rakers (means usually near 10) and 80–150 pyloric caeca (means usually over 100). In contrast, burbot from the Mackenzie system and river systems to the east and south have 7–11 gill rakers (means usually less than 9) and 31–122 pyloric caeca (means usually less than 80). In both characters, as in caudal peduncle shape, there is some evidence of a gradient or cline. *Lota* from the Mackenzie system are usually more like Alaskan burbot than are any of the *Lota* populations to the south or east. Moreover, eastern North American burbot in some respects resemble European burbot more than they do Alaskan burbot.

Although a case can be made here for naming the rather distinctive forms in Alaska and the Great Lakes as separate subspecies, the area of gradual intergradation between them is so great that the utility of such names is questionable. The use of subspecific names based on the present evidence would not only be inconvenient, but it would also imply a particular form of step-wise distribution that does not appear to exist. The problem cannot be resolved without comparison of specimens from over the entire circumpolar range of the species.

Postglacial Dispersal

Burbot were probably present both north and south of the Wisconsin ice sheet. The Alaskan *"leptura"* form spread east and south following deglaciation, and met *"lacustris"* populations spreading northward from one or more southern distribution centres. A refuge may also have existed west of the Continental Divide in the Columbia River basin, perhaps containing an intermediate that had arisen by hybridization during a pre-Wisconsin interglacial period (see "Zoogeographic Patterns"). The present clines in morphological characters may result partly from climatic gradients and partly from the mixture of several stocks of burbot that had been isolated around the ice periphery.

Biology

The burbot is almost the only member of the cod family to invade fresh waters; that it has done so successfully is evident from the distribution map. Although it often lives in deep water, particularly in the south, it also occurs in large rivers, small streams, elevated lakes, and low-lying ponds. In Great Slave Lake it is common at least to depths of 100 m (300 ft). The young are sometimes abundant in streams, and in the shallows of lakes. Seeley (1886) says "It commonly lives under stones and in holes, waiting for its prey, and hence has come, from a rabbit-like habit, to be sometimes named the Coney-fish. Its instincts, however, are those of robber and pirate. It waylays the female and the young brood, especially of the perch, and is a terror to all small fishes." Although Professor Seeley's remarks are a trifle subjective, there is no doubt that the burbot is a voracious carnivore. One 15-inch burbot was found attempting to swallow a 12-inch walleye, and another was found to have 179 fish in its stomach. Fish is its principal diet; in Great Slave Lake burbots had eaten, in order of abundance, ciscoes, cottids, whitefish, sticklebacks, and trout-perch. *Mysis* was the chief nonfish food (about 20%) with small quantities of amphipods, caddis, and sphaeriids (Rawson, 1951). In Heming Lake in Manitoba burbots fed principally on yellow perch, ninespine sticklebacks, and crayfish; in winter the diet was almost exclusively sticklebacks (Lawler, 1962). Burbot evidently feed at night; aquarium specimens are quiescent under bright illumination but forage actively when the light is dimmed. One-year-old burbots in Heming Lake were 147 mm (5.8 inches) long. Great Slave Lake fish were 426 mm (16.8 inches) total length at age 6, and 775 mm (30.5 inches) and 1.7 kg (4.7 lb) at age 16 years.

The burbot spawns in streams or lake shallows under ice, in late winter. Breeding occurs at night, in from 1 to 4 ft (0.3 to 1.3 m) of water, when a number of males and females come together and form a globular mass of squirming bodies. Milt and tiny nonadhesive eggs (about 0.5 mm in diameter) are shed together. One female may lay over a million eggs. The young hatch early in spring.

This intriguing fish has received an extraordinary variety of names, including ling, eelpout, freshwater cusk, maria, metling, loche, lush, dogfish, mother-of-eels, sawyer, and lake lawyer. (This latter name is said to stem from its habit of slippery writhing when one attempts to grasp it.) The name "methye" derives from Cree Indian.

Opinions on utility of the burbot vary widely. Bishop Taché, who seems not to have been enamoured of the fish, wrote in 1870: "At the posts of the interior, the roe is pounded, and made into a kind of biscuit, to which whatever name strikes the fancy is given. The liver, which is rich and delicate, is also made into food, unless it becomes necessary to extract the oil from it for lamps, by which one can only half see, and have, besides, anything but an agreeable smell." On the other hand, Sir John Richardson wrote "When well bruised and mixed with a little flour, the roe can be baked into very good biscuits, which are used in the fur-countries as tea-bread." The liver is in fact rich in vitamins A and D much like cod-liver oil, and is sometimes extracted for medicinal use.

In Alaska burbots were taken in willow traps set in the river current through holes cut in the ice. In Lake Athabasca some are taken in summer by gillnet for dog feed, and in Saskatchewan for mink feed. Burbot caught in shallow lakes in summer have a somewhat muddy flavour, as do pike and other species. From cold water, or in winter, however, burbot meat is white, firm, and delicately flavoured and is attracting an increasing body of sportsmen. During summer burbots are taken most frequently by set lines or nets, whereas in winter they are caught in shallow water by spearing through holes in the ice or on baited hooks hung close to the bottom. One method of skinning the fish is to hang the head on a nail, and seize and strip off the skin with a pair of pliers. The skin, which is tough, with tiny embedded scales, was at one time used in Siberia in place of glass for windows.

THE STICKLEBACKS — Family GASTEROSTEIDAE

Sticklebacks are aggressive little spindle-shaped fishes with sharp spines ahead of the soft dorsal fin and in the pelvic fins. They lack ordinary scales, usually having some bony plates along the side and on the slender peduncle. Some are marine and some freshwater. All build nests into which the male entices the female after a stereotypes courtship. After the eggs are laid and fertilized, the male guards the nest until the young emerge. Sticklebacks will build nests and reproduce readily in an aquarium, and have been studied intensively by scientists throughout the northern hemisphere. Some occur in the north in sufficient concentration to be taken as dog or even human food.

There are 5 genera and about 10 species of sticklebacks, ranging across Europe, northern Asia, and North America. Three enter our area.

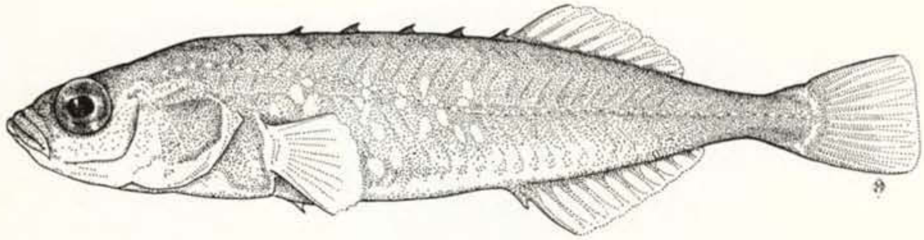
KEY TO THE SPECIES

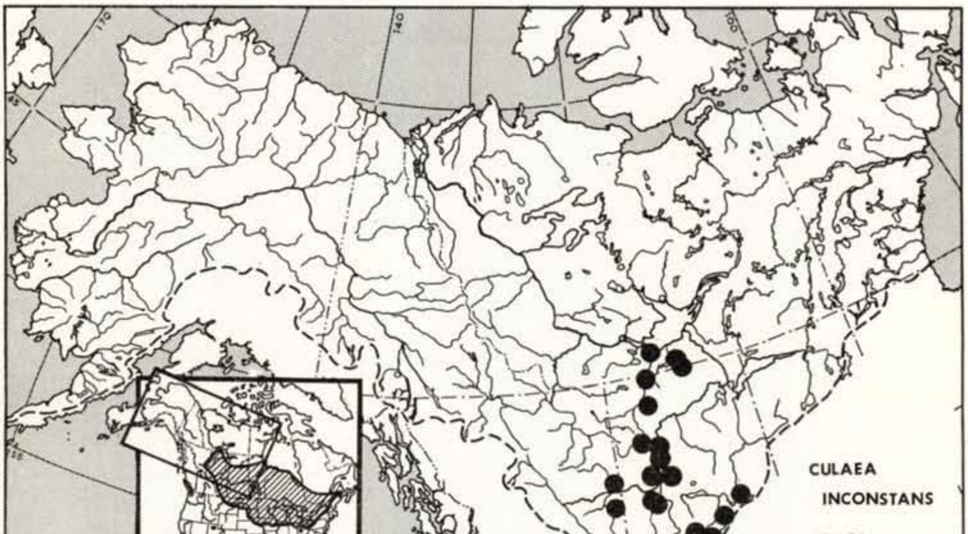
1(2) Two to four spines before soft dorsal fin; gill membrane fused to the isthmus ....Threespine stickleback, *"Gasterosteus aculeatus"* complex .... (p. 311)

2(1) Five or more spines before soft dorsal fin; gill membrane free from the isthmus 3

3(4) Five to seven dorsal spines; no keel on the caudal peduncle .... Brook stickleback, *Culaea inconstans* (Kirtland) (p. 303)

4(3) Seven to twelve dorsal spines; a well-developed keel on the caudal peduncle .... Ninespine stickleback, *Pungitius pungitius* (Linnaeus) (p. 307)




CULAEA
INCONSTANS
0 MILES 400
0 KILOMETRES 600

BROOK STICKLEBACK

Culaea inconstans (Kirtland)

Culaea is a name coined to replace the original name *Eucalia* when it was found to have been applied previously to a butterfly, and *inconstans* means *variable*. The French common name for this species is *épinoche à cinq épines*.

Distinguishing Characters

The 5–7 closely set spines before the soft dorsal fin, and the lack of a keel on the peduncle.

Description

Body elongate, spindle-shaped; head short, about one-quarter total length; snout short; eye small, less than snout length. Mouth small, oblique; lower jaw projecting; numerous small teeth on premaxillary and dentary; caudal peduncle narrow, about equal to vertical eye diameter. Branchiostegals 3 + 3; gill rakers slender, 2–3 + 9–12; 5–7 short dorsal spines; 8 or 9 dorsal rays; one anal spine and 8–10 anal rays; 10 pectoral rays; and 1 pelvic spine and 1 ray. No scales, but minute bony plates are associated with the 29–34 pores in lateral line. Vertebrae 30–34. No pyloric caeca.

Size: To 65 mm (about 2.5 inches).

Sexual dimorphism: No obvious external differences between sexes except colour at spawning time.

Colour: Adults are dark olive green above, mottled on the sides, and pale below. The membranes on the free dorsal spines are often dark, but the rest of the fins are pale. In breeding males the lower body and sometimes the fins are jet black. Breeding females are characteristically pale with a pattern of brown speckles on the back and sides.

Distribution

Found only in North America; from the upper Mississippi and Missouri systems north to the south shore of Great Slave Lake, and from the foothills of the Rocky

Mountains east to New Brunswick. It is reported in brackish waters from James Bay. In our area the brook stickleback is known only from the Mackenzie system south of Great Slave Lake, and slightly west of the British Columbia–Alberta border.

Taxonomic Notes

The brook stickleback was originally described from Ohio as *Gasterosteus inconstans* by Kirtland in 1841. The generic name was changed to *Eucalia* by Jordan in 1876, and until recently the brook stickleback was called *Eucalia inconstans*. However, Whitley (1950) noted that the name *Eucalia* was preoccupied as a generic name in butterflies, and proposed a new generic name, *Culaea*. Synonyms include *micropus, globiceps,* and *pygmaeus.*

Postglacial Dispersal

The present range of the brook stickleback includes only one unglaciated area, the upper Mississippi Valley. All of the populations in our area were derived by postglacial dispersal from this refuge.

Biology

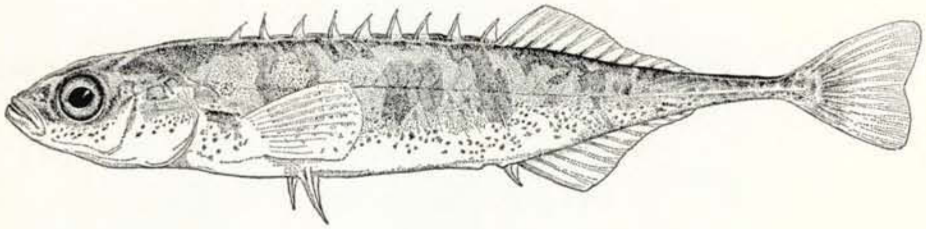
The brook stickleback is usually found in slow streams or shallow lakes and bays. It is almost invariably associated with dense aquatic vegetation. In such areas large aggregations of brook sticklebacks swim quietly around weed beds or lurk almost motionless in the dense vegetation. They swim slowly, except when startled, and often scull with the pectoral fins in such a manner that they appear to glide through the water. They often remain motionless, their bodies at about a 45° angle to the bottom, and stare fixedly at the bottom. Occasionally, they will suddenly dart to the bottom and seize some food item. This may be chewed, spat out, seized, chewed some more, and spat out several times before finally being swallowed. Brook sticklebacks are carnivorous, feeding largely on insect larvae, ostracods, small crustaceans, and molluscs. They appear to feed mainly on bottom organisms or animals closely associated with the bottom. However, they are apparently not above robbing each other's nests, and in the spring it is not uncommon to find them with stickleback eggs in their stomachs.

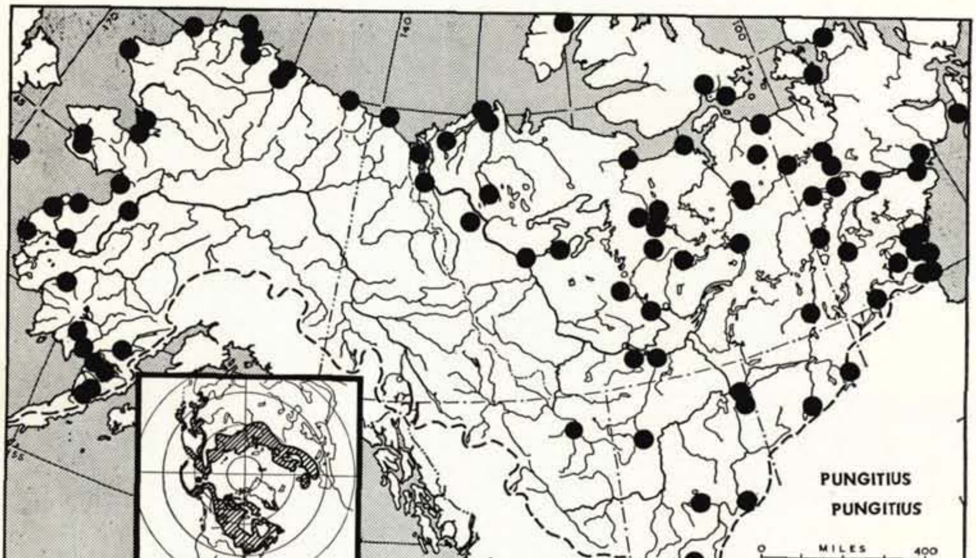
Nothing is known about the age and growth of brook sticklebacks in our area. Farther south they grow rapidly and reach sexual maturity in 1 year. Spawning occurs in the spring (April to June in Michigan) and in our area appears to continue into July. A ripe female, and several with maturing eggs, were taken on July 2 in Charlie Lake, B.C. Male brook sticklebacks move into shallow water in the spring. In a small Ontario stream tributary to Georgian Bay spawning was followed by a striking downstream migration in June or July, during which the majority of fish moved towards the lake within a few days (Lamsa, 1963). Like other sticklebacks, this species is territorial; the male defends its territory against other males and other fishes. The male constructs a nest by glueing together bits of algae, small sticks, and debris. The kidneys are modified to produce a sticky substance. The nest is normally built among vegetation, and is usually attached to an aquatic plant. It is commonly built about 15 cm off the bottom but often is close to, or even on, the bottom. When first constructed the nest has a single entrance.

When a gravid female brook stickleback enters the territory of a male, the male stiffens, erects his spines, and slowly positions himself so that he is pointing directly at the female. At this time he manoeuvers mainly with his pectoral and caudal fins. The female is usually below the male and the male is tilted, head down, at an angle towards the female. The male slowly advances towards the female and then suddenly darts at her, striking her with his head. He may then back off and repeat this procedure several times. With these attacks the female stops swimming and sinks passively to the bottom. Now, after striking the female, the male suddenly turns away, rigidly arches his body, and with all spines erected sculls with his pectoral and caudal fins towards the nest. Usually this procedure is repeated several times before the female follows him to the nest. When the female follows, the male swims directly to the nest and presses his mouth against the upper rim of the nest entrance. The female then enters the nest and the male quivers alongside that portion of her body that is out of the nest. The female may quiver several times in the nest while the eggs are being extruded. The female then leaves the nest, often forcing her way through the end of the nest, and the male enters and fertilizes the eggs. The male then drives the female off, and will often mend the hole torn in the nest. He then guards the nest and fans the developing eggs. In the brook stickleback the male begins fanning immediately after fertilization, and it is continued throughout development, although the intensity of fanning drops off in the first few days and then increases again later in development. When the young emerge from the nest the male attempts to return them to the nest. This continues until the larvae have developed to a point at which the male can no longer effectively retrieve them.

The eggs of the brook stickleback are quite large (about 1–1.5 mm in diameter) and sticky. A female usually lays 40–80 eggs at one time, but probably spawns more than once in a season. The eggs of more than one female may be laid in the nest of one male.

Brook sticklebacks are valuable as forage for such large predatory fish as pike and walleyes. They make excellent aquarium fishes as they are easy to keep and will spawn readily in a suitable aquarium.





PUNGITIUS
PUNGITIUS
MILES
400
KILOMETRES
600

NINESPINE STICKLEBACK

Pungitius pungitius (Linnaeus)

Pungitius means *pricking.* The French common name for this species is *épinoche à neuf épines.*

Distinguishing Characters

The 7–12 closely set spines before the soft dorsal fin (the space between the spines is less than the length of the spines), and the narrow caudal peduncle with a keel.

Description

Body long, slender; head short, less than one-quarter total length; eye larger than in *C. inconstans*, about equal to snout. Mouth small, oblique; lower jaw projecting; numerous small teeth on premaxillary and dentary. Caudal peduncle very narrow, usually less than one-half vertical eye diameter, and with a well-developed bony keel on either side that extends forward almost to the origin of the soft dorsal. Branchiostegals 3 + 3; gill rakers slender, 10–15; 7–12 dorsal spines; 9–13 dorsal rays; one anal spine and 8–11 anal rays; 10 or 11 pectoral rays; and 1 pelvic spine and 1 ray. No scales; 0–8 very small bony plates on anterior portion of lateral line (in some Atlantic coast populations there are bony plates along the entire body). Vertebrae 31–35. No pyloric caeca.

Size: To 90 mm (about 3.5 inches).

Sexual dimorphism: No obvious external differences between sexes except colour at spawning time.

Colour: In adults olive green to light brown on the back, sides irregularly barred or mottled with the same colour, underparts yellowish white, fins immaculate. In breeding season males are jet black under the chin and along the belly, and the membranes of the ventral spines are white.

Distribution

Lowland areas in Europe, Asia, and North America. In Eurasia from France (Loire River) north and east along coastal regions to the Chukotsk Peninsula, Siberia, and south along the Pacific coast of Asia to Japan (vicinity of Kyoto) and Korea. The genus extends farther south in Asia (to the Yangtse River, China), but the taxonomic relationships of these forms (*P. tymensis* and *P. sinensis*) to *P. pungitius* is uncertain. In central Europe the genus is represented in the Caspian–Aral area by another species, *P. platygaster*. In North America from Cook Inlet, Alaska, north along the coast to the Mackenzie Delta (in these areas it does not penetrate far inland); throughout much of the Mackenzie system including Fort Nelson, B.C., and most of the rivers and lakes of north-central Canada south to the Saskatchewan system; also throughout most of the arctic Archipelago and the coastal regions of Hudson Bay and Labrador, and on Baffin Island and Greenland; south on the Atlantic coast to New Jersey, and east to Sable Island off Nova Scotia and to the eastern tip of Newfoundland; present in the Great Lakes, except Lake Erie, and in two isolated populations in the upper Mississippi Valley.

Taxonomic Notes

The ninespine stickleback was originally named from Europe as *Gasterosteus pungitius* by Linnaeus in 1758. Many European authors use the generic name *Pygosteus* for the ninespine stickleback. However, *Pungitius* Costa 1846 has priority, and the correct scientific name for the ninespine stickleback is *Pungitius pungitius.*

There is considerable geographic variation in the number of dorsal spines and other characters in North American populations. This variation has a distinct geographic pattern (McPhail, 1963). Coastal populations tend to have more lateral plates, more dorsal spines, and fewer gill rakers than do inland populations. Although the differences are not sufficient to warrant subspecific recognition, they are useful in determining postglacial dispersal routes.

Postglacial Dispersal

McPhail (1963) has postulated that the two morphological forms of *P. pungitius* in North America arose by isolation in two ice-free areas (the Bering and Mississippi glacial refuges) during the last glacial period. The Bering form is found throughout much of the Bering refuge area, and has dispersed postglacially southward into the Gulf of Alaska and eastward along the arctic coast to Hudson Bay and right around to the Atlantic coast. The Mississippi form is found in the upper Mississippi Valley and the Great Lakes region, and postglacially has dispersed to the northwest across the northern Great Plains.

Biology

The ninespine stickleback is typically found in shallow bays of lakes, slow streams, and tundra ponds. Dense aggregations may be associated with heavy aquatic vegetation. However, in our area, small numbers are often found over sand or even gravel beaches and other areas of sparse vegetation. Coastal ninespine sticklebacks (which probably differ genetically from inland populations in habits as well as structure (T. Narita, personal communication)) are often abundant in estuaries, but in our area are relatively rare in totally marine habitats. However, we have taken occasional individuals in the sea, even in such unlikely habitats as the surf-pounded sand beaches near Nome, Alaska. In the vicinity of Churchill, Manitoba, ninespine sticklebacks in summer appear to be confined to the lower portions of streams (where they nest) and to freshened portions of Hudson Bay in the immediate vicinity of stream mouths. In this region the coastal forms, which have a higher salinity tolerance than the inland forms, evidently spend the winter in the sea (T. Narita, personal communication).

Like other sticklebacks, *Pungitius* swims rather slowly, unless disturbed, and often sculls with the pectoral fins causing the fish to glide smoothly through the water. The ninespine stickleback is carnivorous and feeds mainly on bottom organisms such as insect larvae, small crustaceans, ostracods, and molluscs. However, at some times of the year it may feed heavily on winged insects and the eggs of other sticklebacks.

Nothing is known about the age and growth of ninespine sticklebacks in our area. Farther south and in Europe they reach sexual maturity after 1 year and may live as long as 3 years.

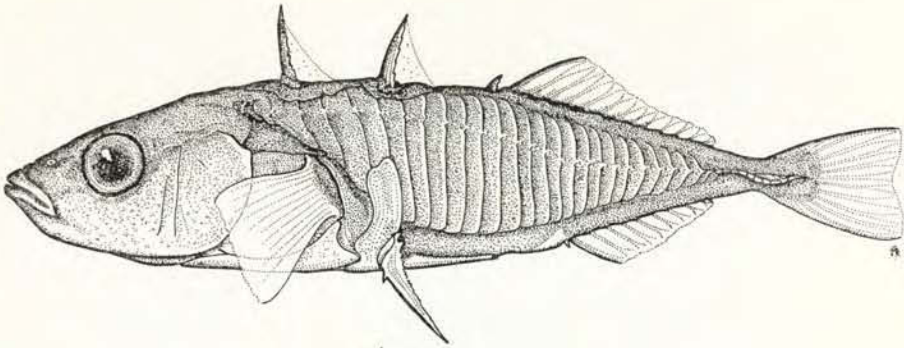
Spawning occurs in the spring and summer. In our area, breeding populations of *Pungitius* have been noted from May to late July. Spawning is usually associated with dense vegetation, although coastal fish near Churchill have been observed to build nests on the bottom in more exposed sites. It is not known whether the ninespine stickleback is capable of breeding in pure sea water.

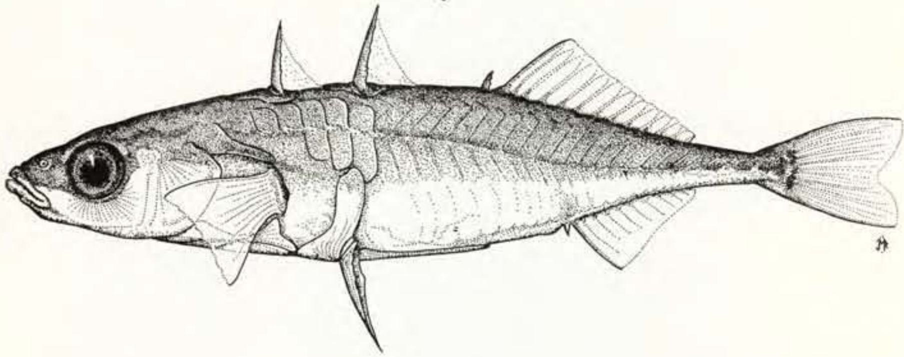
Like other sticklebacks, *Pungitius* is territorial and the male builds a nest. The nest is constructed of algae and debris from aquatic plants; it is normally tunnel-shaped. The nest is typically built in dense vegetation and is usually 10–15 cm off the bottom, but occasionally is in contact with the bottom. When a ripe female enters the territory of a male, the male assumes a position in which his head is pointing downwards at an angle. Then, still in this head-down position but with spines erected, he swims toward the female in a series of abrupt sideways jumps known as the zig-zag dance. When close to the female he may suddenly attack her, or simply dart at her without actually touching her. The male then turns away and dances towards the nest. The female may then respond by taking a peculiar head-up posture (she swims with her head up and her tail down), and follows the male to the nest. When the male reaches the nest he places his snout just inside the rim of the entrance and begins to fan with his pectoral fins. The female then pushes past him and enters the nest. The male shivers along side of her tail and this apparently stimulates the female to release her eggs. The male then enters the nest and fertilizes the eggs. When he emerges from the nest he attacks the female and drives her away if she is still in the vicinity of the nest. The male then begins to fan the eggs and continues fanning them throughout development.

The eggs hatch in about 7 days at 18 C (64.4 F). After the eggs hatch and the larvae are able to swim, the male may transfer them to a nursery area. The nursery area is usually a loosely constructed aggregation of nest-building material situated directly above the nest. After a few days in the nursery area the young are completely free-swimming and disperse. The male may then construct a new nest and begin to court females again.

The eggs of the ninespine stickleback are about 1–1.5 mm in diameter and sticky. A gravid female lays from 30 to 80 eggs at a time, but probably spawns more than once in a season.

Ninespine sticklebacks serve as forage for larger species such as pike, lake trout, arctic char, and grayling. Although small, they occur in such abundance at some times of the year in the Yukon and Kuskokwim delta regions that they are trapped by the natives and used for human food. Like other sticklebacks they make excellent aquarium fishes.






"GASTEROSTEUS
ACULEATUS"
COMPLEX
TRACHURUS
LEIURUS
MILES
KILOMETRES

THREESPINE STICKLEBACK

"Gasterosteus aculeatus" complex including *Gasterosteus aculeatus* Linnaeus

Gasterosteus means *belly bone* and *aculeatus* means *spined.* The French common name for this species is *épinoche à trois épines.*

Distinguishing Characters

The two (occasionally three) large, well-separated dorsal spines, followed by a smaller dorsal spine immediately in front of the dorsal fin, and the strong pelvic spines usually extending to within an eye-diameter of the anus; gill membranes attached to the isthmus.

Description

The fishes here referred to as *Gasterosteus aculeatus* probably represent a complex of species. Their taxonomy and relationships are confused, and the reader should refer to the "Taxonomic Notes" section for details. There are two morphologically different forms of *Gasterosteus aculeatus* in our area: a heavily plated form that is usually marine (called *trachurus*) and a partially plated freshwater form (called *leiurus*). In Alaska and along the western shore of Hudson Bay both forms occur in some lakes and therefore both forms are included in the description. In addition an intermediate form (*semiarmatus*) is often taken in areas where the other two forms occur sympatrically.

Body deep, compressed; head short, about one-quarter total length; snout short. Mouth small, oblique; lower jaw projecting; numerous small teeth on the premaxillary and dentary. Branchiostegals 3 + 3; gill rakers long, slender, 17–25 in the unplated form and 19–26 in fully plated form; 3 or 4 dorsal spines, the first two much longer than the others; 10–14 dorsal rays; 1 anal spine, 6–10 anal rays; 9–11 pectoral rays; 1 long serrated pelvic spine, and 1 pelvic ray. No scales, usually 4–8 bony plates on the side of the body in the purely freshwater form and 22–37 plates in the anadromous form. In waters where both forms occur there may be intermediates, but these are always less common than the other forms. A sharp-edged bony keel is present on either side of the caudal peduncle of anadromous fish. Vertebrae: 30–34; 1 or 2 short pyloric caeca.

Size: Total length to 75 mm (about 3 inches).

Sexual dimorphism: No obvious external differences between sexes except colour at spawning time.

Colour: In freshwater populations the adults are olive green to dark brown on the back and sides, and the underside is light yellow, white, or silvery. The fins are pale. Breeding males are red below (often very bright) and blue along the sides. The iris of the eye in breeding males is iridescent blue or green. In breeding females the throat and belly are sometimes a dull pink, but more typically silvery.

Distribution

Europe, Asia, and North America; in North America the range is disjunct: Baja California to St. Lawrence Island, Alaska, and Chesapeake Bay to Cumberland Sound, and Nettilling, Baffin Island; also Richardson (1855) took *"Gasterosteus insculptus"* from Northumberland Sound (northwest Devon Island) in a nonclosing deepwater net. In our area completely freshwater populations of the threespine stickleback extend north only to the Bristol Bay region, Alaska, and in the eastern Canadian Arctic to Baffin Island. On the west shore of Hudson Bay both marine and freshwater forms occur north at least to Maguse River.

Taxonomic Notes

The threespine stickleback was first described as *Gasterosteus aculeatus* by Linnaeus in 1758. It is not known whether this description was based on fully plated or partially plated specimens. The first valid name for the partially plated form without a caudal keel is probably *Gasterosteus leiurus* Cuvier and Valenciennes 1829, named from the Seine River in France. In the Pacific, the first available name for the fully plated form is *G. cataphractus* Pallas 1811 (from Kamchatka) and for the partially plated form without a caudal keel, *G. microcephalus* Girard 1856.

There are two basic problems that confuse the taxonomy of the *G. aculeatus* complex. The first is the relationship between the Atlantic and Pacific populations, and the second is the relationship between the basically marine fully plated form and the freshwater partially plated form without a caudal keel. At present, there are vast disjunctions between the ranges of *G. aculeatus* in the Atlantic and Pacific areas. There is no possibility of gene flow between these areas, but no one knows how long these disjunctions have existed. If they existed previous to the last (Wisconsin) glaciation, then the present practice of treating the Atlantic and Pacific populations as identical may be a dangerous oversimplification. A detailed comparison (including morphological, ethological, physiological, and ecological aspects) of Atlantic and Pacific populations is greatly needed. Several isolated populations along the

Pacific coast of North America are now being studied, and they indicate that in this area alone several species probably exist.

The relationship between the fully plated marine form and the partially plated freshwater form is even more complex. These forms are referred to here by the names *trachurus* (the fully plated usually marine form) and *leiurus* (the weakly plated freshwater form). These names are used only for convenience and are intended to imply no taxonomic status. The *trachurus* and *leiurus* forms (and their hybrid *semiarmatus*) are widespread in both the Atlantic and Pacific areas. On the Pacific coast of North America the relationship between these two forms has been examined in detail in one small river (the Little Campbell River in southwestern British Columbia). This study (Hagen, 1967) indicates that although hybrids between the two forms are common, they are extremely rare outside of a narrow hybrid zone. Hagen arrays strong arguments that the *trachurus* and *leiurus* forms should be treated as distinct species. The presence of the strictly freshwater *leiurus* on many offshore islands (such as the Aleutian and Pribilof islands) compels us to conclude that *leiurus* has evolved independently in a number of different localities. This is not a unique situation (see the discussion of *Myoxocephalus quadricornis*), but it does pose a nomenclatural problem. What name, or names, should be applied to these independently evolved freshwater forms? For the present we use the term "*G. aculeatus*" complex but recognize that this may include very different animals. An effort should be made always to describe in detail the form to which the name is being applied.

Postglacial Dispersal

On the Pacific coast of North America the range of "*G. aculeatus*" complex includes at least two unglaciated areas: the Bristol Bay region of Alaska, and the unglaciated portions of the coast south of the maximum extent of the Cordilleran ice sheet. The threespine stickleback probably survived glaciation in both refuges. In the western part of our area the populations of *G. aculeatus* are probably all derived from those that survived in the Bristol Bay region. On the Atlantic coast of North America the range of *G. aculeatus* includes only one unglaciated area, the northern portion of the unglaciated Atlantic Coastal Plain. The threespine sticklebacks in the eastern part of our area were derived by postglacial dispersal from the Atlantic Coastal Plain northward along the coast of Labrador and then west into Hudson Bay.

Biology

The following notes on the biology of the threespine stickleback mainly refer to the freshwater form. Major differences that are known to occur between the freshwater and marine forms are noted.

The threespine stickleback is typically an inhabitant of shallow bays and slow streams. It is usually found associated with aquatic vegetation, but this association is not as strong as in other sticklebacks. In the large lakes of the Bristol Bay region, Alaska, dense populations of sticklebacks often are found living over deep water. The marine form appears to be primarily pelagic; little is known of the extent of their migrations in the sea during winter, but a number have been captured at the surface some 500 miles from land in the Gulf of Alaska. In shallow water the threespine sticklebacks swim rather slowly, characteristically sculling with their pectoral fins, and tend to be benthic feeders (ostracods and insect larvae are the main items in their diet). Pelagic populations feed mainly on planktonic organisms. Freshwater populations in Alaska mature in their 1st or 2nd year and live a maximum of 3 years (Greenbank and Nelson, 1959). The marine form probably matures in 1 year, and, although there is a considerable mortality after spawning, some individuals may spawn a 2nd year.

The threespine stickleback is territorial during the breeding season, and like other sticklebacks it builds a nest of algae and debris from aquatic plants. The male digs a hole in the bottom mud (sand in the case of the marine form) and glues algae together to form the nest. The nest is usually built near aquatic plants, but is more exposed than the nests of other sticklebacks. There are persistant rumours of some northern populations building nests entirely of sand, but this has not been verified. Freshwater populations spawn in the spring and summer (May through July) in Alaska. The marine populations enter fresh water in the late spring (June) and spawn shortly after. When a gravid female enters the territory of a male, the male swims rapidly up to her and begins to jump abruptly from side to side (the zig-zag dance). In many western North American populations the zig-zag dance is not as obvious as it apparently is in European populations. In such western populations the zig-zag dance is a barely perceptable series of side-to-side head motions. However, in the threespine sticklebacks that we have observed there has been considerable variation in the male courtship, and we suspect that the courtship of *Gasterosteus* is not as stereotyped as is sometimes indicated. If the female is ready to spawn she responds to the male's courtship by performing a head-up motion. In this position the female's head is up and her distended abdomen is displayed to the male. The male then swims rapidly to the nest and the female follows. If the female does not follow, the male will usually go to the nest alone and fan or glue (a position in which the male arches over the nest and expels glue from the kidneys) before returning to court the female again. When a female is led to the nest, the male shows the nest by thrusting his snout into the entrance and vibrating rapidly back and forth. The female then crowds in beside him and the male rolls over on his side. The female then pushes into the nest and the male swims to the side of the nest and jabs his snout through the nest. He then performs a series of rapid jabbing motions with his snout pressed against the side of the female. This apparently stimulates the female to release her eggs. The female then leaves the nest and the male swims through the nest fertilizing the eggs as he goes. When he emerges he attacks the female and drives her off. The male then begins to fan the nest, and continues to fan with increasing frequency until just before the eggs hatch. Hatching occurs in about 7 days at 18 C (64.4 F). A few days after the eggs hatch the young emerge from the nest and the male is kept busy catching them and returning them to the nest. When the young are completely free-swimming they remain in a dense school around the male for a short time, but eventually disperse. The male may then build a new nest and the cycle begins again. It is not uncommon for a male to have more than one set of eggs (at different stages of development) in the nest at one time. The eggs of the threespine stickleback are larger (about 2 mm in diameter) than other sticklebacks and are sticky when laid. A gravid female lays from 50 to 200 eggs at a time, and a single female will often spawn several times in a season.

Threespine sticklebacks are important forage for large predaceous species like arctic char, Dolly Varden, lake trout, and pike. In addition, the dense pelagic populations in some of the Alaska salmon lakes may have an important effect on the growth rate of young sockeye salmon. Like other sticklebacks they are excellent aquarium fishes, and an opportunity to observe their courtship is well worth the little effort needed to maintain them in an aquarium.

THE SCULPINS — Family COTTIDAE

The sculpins are small bottom dwellers with broad flat heads and big pectoral fins. There is a spiny fin and a soft dorsal fin, and one or more spines on the preopercle. The body may be prickled, plated, scaled, or naked. Most of the several hundred species are marine, but one genus (*Cottus*) has successfully invaded fresh water in North America and Eurasia, where it forms many variable and puzzling species. *Cottus* spawns in spring; the egg masses are attached under stones, and guarded by the male. There are over 20 North American species of *Cottus*, four of which enter our area. In addition, *Myoxocephalus quadricornis* has freshwater as well as marine populations.

KEY TO THE SPECIES

1(8) Gill membrane broadly attached to isthmus (Fig. 24A); dorsal fins touching or scarcely separated 2

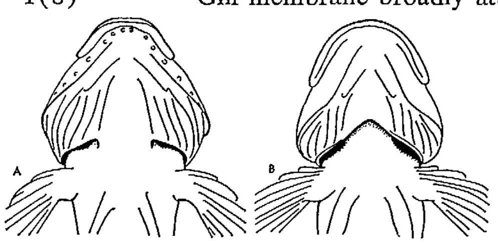


Fig. 24. Ventral views of sculpin heads. A, *Cottus cognatus;* B, *Myoxocephalus quadricornis thompsoni.*

2(7) Tubular portion of lateral line complete; one pore on midline at tip of chin (Fig. 25) 3

3(4) Palatine teeth present (Fig. 25); 16–19 (rarely 15) anal rays .... Prickly sculpin, *Cottus asper* Richardson (p. 325)

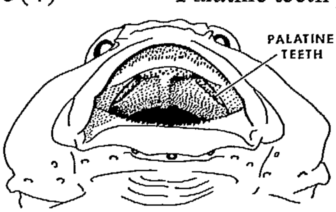


Fig. 25. Front view of head, *Cottus asper.*

4(3) Palatine teeth absent; 12–15 anal rays 5

5(6) Head very wide, and flattened in profile; prickles usually heavy, covering most of body; uppermost spine on preopercle long, curved inward, its length more than two-thirds eye diameter .... Spoonhead sculpin, *Cottus ricei* (Nelson) (p. 337)

6(5) Head rounded in profile; prickles restricted to patches behind pectoral fins; upper preopercular spine about one-half eye diameter, not strongly curved inwards .... Coastrange sculpin, *Cottus aleuticus* Gilbert (p. 329)

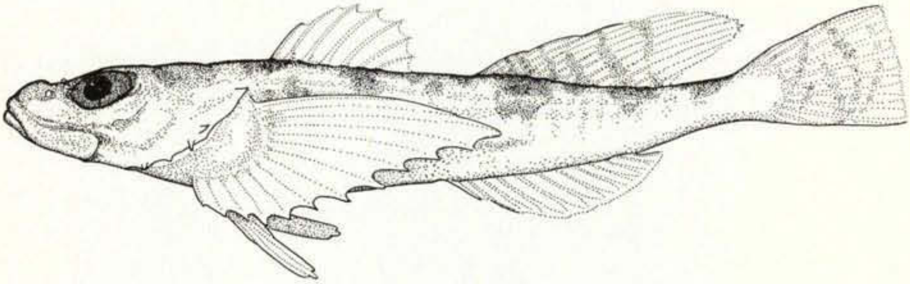
7(2) Tubular portion of lateral line ends ahead of centre of 2nd dorsal fin, although there may be pores beyond this point; two pores on midline at tip of chin (Fig. 24A) .... Slimy sculpin, *Cottus cognatus* Richardson (p. 333)

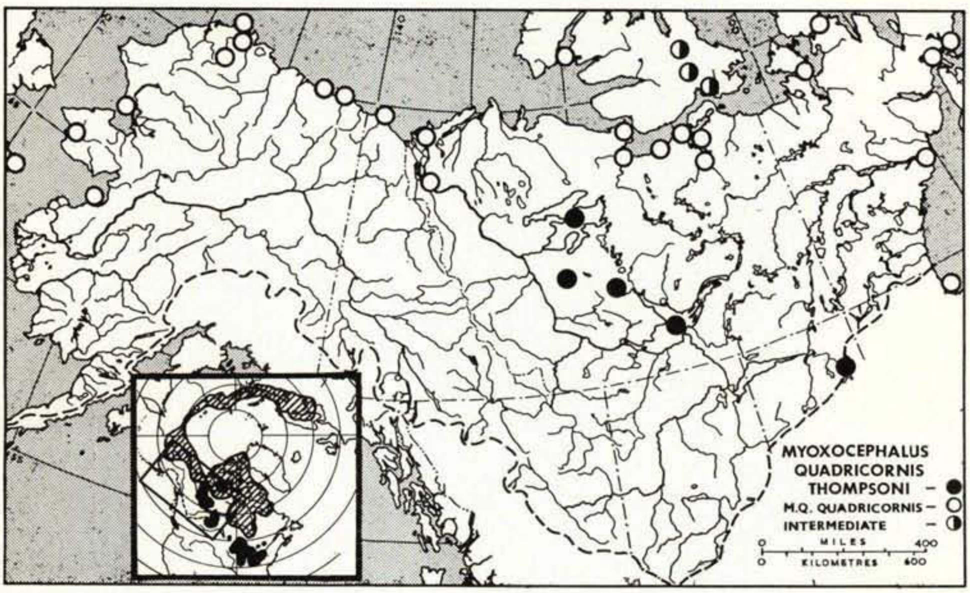
8(1) Gill membrane free from isthmus (Fig. 24B); dorsal fins distinctly separated 9

9(10) No tubercles below lateral line; usually 30 or fewer tubercles above lateral line; rarely over 90 mm (3 inches) total length .... Deepwater sculpin, *Myoxocephalus quadricornis thompsoni* .... (Girard) (p. 319)

10(9) Almost always some tubercles below lateral line; usually 31 or more tubercles above lateral line .... Fourhorn sculpin, *Myoxocephalus quadricornis quadricornis* .... (Linnaeus)

This is the large marine relative of *M. q. thompsoni*, which occasionally ascends arctic rivers for some distance.




MYOXOCEPHALUS
QUADRICORNIS
THOMPSONI
M.Q. QUADRICORNIS
INTERMEDIATE
MILES
400
KILOMETRES
600

DEEPWATER SCULPIN

Myoxocephalus quadricornis thompsoni (Girard)

Myoxocephalus means *head like a dormouse*; *quadricornis* means *four horned*; and *thompsoni* is named after Rev. Zadock Thompson, author of the History of Vermont. The French common name for this species is *chabot de profondeur*.

Distinguishing Characters

The gill membrane free from the isthmus, and disklike tubercles on the upper sides. The two dorsal fins are distinctly separated, whereas in *Cottus* they are almost confluent.

Description

Body elongate, stout anteriorly and very slender at the caudal peduncle; head large and flat, about 3–3.8 times into the standard length; eye small, usually about three-quarters snout length. Mouth large, somewhat oblique; small teeth in both jaws and on the vomer. Four well-developed preopercular spines, the dorsal-most preopercular spine large, usually 4.5% or less of the standard length in mainland freshwater populations (in Victoria Island freshwater populations the longest preopercular spine ranges from 3.8 to 5.8% of the standard length). Frontal, parietal, and cleithral spines are usually absent or weakly developed in mainland freshwater populations but are better developed in Victoria Island freshwater populations. Branchiostegals 6–6, a continuous membrane uniting the two sides, its margin free from the isthmus (Fig. 24B). Gill rakers short and stubby, usually 5–8. Two dorsal fins, distinctly separated, the first with 7–10 spines and the second with 11–16 soft rays; 11–16 anal rays; 15–18 pectoral rays; and 1 spine and 3 rays in the pelvic fins. No scales; in freshwater populations there are no tubercles below the lateral line, and usually fewer than 30 above the lateral line; lateral line usually complete. About 40 vertebrae, and 5–9 pyloric caeca.

Size: To 200 mm (8 inches) in the south, but only recorded to 69 mm (2.7 inches) standard length in our area.

Sexual dimorphism: The second dorsal fin is much higher in mature males and usually reaches the base of the caudal fin when depressed. In mature females the second dorsal is not notably enlarged. The pelvics are also notably longer in males than in females. There are small tubercles on the rays of the second dorsal and pectoral fins in males; in females these are usually absent or weakly developed.

Colour: Head dark grey or brown; about seven diffuse dark saddles along back; dark brown saddle on caudal peduncle and caudal base. Sides yellowish, belly and pelvics white; chin and undersurface of head with heavy dark speckling. Pectorals with three diffuse dark bands; dorsal and anal fins with faint dusky blotches, caudal with dark brown mottling.

Distribution

The species is circumpolar in cold brackish waters, with freshwater derivatives in Eurasia, on mainland North America, and on Canadian Arctic islands. The marine form occurs in the Baltic Sea and along the Eurasian Arctic Ocean coast from Murmansk east to Bering Strait; south in Bering Sea to Anadyr River and in Labrador south to 56°32′; many islands of the Canadian Arctic Archipelago including northern Ellesmere (within 500 miles of the North Pole); eastern Greenland south to 70°N. The marine form may move some distance into rivers; it has been taken 80–90 miles up the Meade River in Alaska, 120 miles up the Mackenzie River at Arctic Red River, and in a stream draining Elinor Lake on Cornwallis Island. A series of freshwater forms occur in European waters bordering the northern Baltic Sea. In North America freshwater forms have been found on Victoria Island and in the following mainland lakes: Great Bear, Keller, La Martre, Great Slave, Wollaston, Reindeer, La Plonge, La Ronge, Mackay, Mirond (in Saskatchewan west of Flin Flon), Athapapuskow (in Manitoba south of Flin Flon), West Hawk (southeastern Manitoba), Cedar (Algonquin Park), Heney (50 miles north of Ottawa), Torch (Michigan), and all of the Great Lakes.

Taxonomic Notes

Linnaeus named *Cottus quadricornis* from the Baltic Sea in 1758. Several other species named from the north, including *polaris* from the east side of Boothia Peninsula, *hexacornis* from Tree River, N.W.T., and *labradoricus* from Labrador, have subsequently been reduced to subspecies of *quadricornis*, which is now generally placed in the genus *Myoxocephalus.* Walters (1955) argued that the three marine subspecies of *Myoxocephalus quadricornis* recognized by Berg (1948–49) were based on unreliable characters. Walters used no subspecific name, but concluded that if an American marine subspecies were recognized as distinct from the European it must be *M. quadricornis polaris* (Sabine). If, as seems advisable at present, all marine forms are considered to be in the same subspecies, it should be called *M. quadricornis quadricornis* (Linnaeus).

Apart from the question of whether the marine forms should be broken into several subspecies, there remains the difficult problem of nomenclature for the freshwater derivatives.

In lakes adjacent to the Baltic Sea, and also in lakes of North America, a smaller purely freshwater form occurs, usually in deep water. McAllister (1961) compared North American mainland freshwater specimens with marine specimens. Principal distinguishing characters of the freshwater form were the shorter preopercular spine (4.5% or less of standard length), frequent absence of cleithral, frontal, and parietal spines, and the absence of tubercles below the lateral line. These characters used in combination allowed complete separation between all individuals examined by McAllister.

This distinctive form from deep North American lakes was first named *Triglopsis thompsoni* by Girard in 1852, based on Lake Ontario specimens. All recent authors agree that there is no valid difference between the genera *Triglopsis* and *Myoxocephalus*. McAllister (1961) concluded that the freshwater form was specifically different from its marine progenitor, and used the name *Myoxocephalus thompsoni*. We are following Nikolsky (1961) and Hubbs and Lagler (1964) in considering the freshwater form as only subspecifically different from the marine; hence the name *M. quadricornis thompsoni* (Girard).

Our reasons for this course, despite McAllister's (1961) data, are that Johnson (1964) has since discovered populations in three lakes on Victoria Island that are in some respects intermediate between previously known North American marine and lake forms. We are thus faced with the following range of forms: (*a*) large fish, with long preopercular spines, etc., in the sea; (*b*) large long-spined fish that have moved considerable distances into fresh water (perhaps temporarily) in Meade River, Mackenzie River, and Elinor Lake outlet on Cornwallis Island; (*c*) small fish with intermediate spines in lakes on Victoria Island; (*d*) small short-spined fish in mainland lakes, some well south of the present range of the marine fish. Somewhat comparable series of forms occur in Europe.

Probably the marine form has given rise to freshwater derivatives in several places and at several times; the process may well be continuing. Because we have no evidence that the two may occur sympatrically without interbreeding, and because the extreme forms seem joined by a continuum of morphological intermediates, we feel obliged to recognize only one species. On the other hand, the form inhabiting North American lakes seems to fulfill the criteria for subspecies described by Bailey et al. (1954), in that it displays a high degree of uniformity over a wide range and differs with high constancy from the marine form, with intermediates occurring only in a limited region.

There is insufficient information to decide whether European freshwater "relict" populations differ greatly from those in North America. Spine development may differ somewhat. Spawning time of both marine and freshwater forms is said to be in winter in Europe but in summer in North America (McAllister, 1961). In any event the name *thompsoni* has priority over any of the subspecific names applied to Palearctic relicts of the species.

We use the common name "deepwater sculpin" for *M. q. thompsoni* because it habitually occurs at much greater depths (in mainland fresh water) than does its marine counterpart (McAllister, 1961). The fish from lakes on Victoria Island are smaller than the marine form and probably reproduce in fresh water; morphologically they lie between the mainland freshwater and the marine forms, but they more closely resemble the former. They may most conveniently be considered as *M. q. thompsoni*, although this decision is on phenetic rather than phyletic grounds, since the Victoria Island fish probably evolved from marine ancestors much more recently than did the southern deepwater fish.

Postglacial Dispersal

This species has probably colonized North American fresh waters in more than one way. On the mainland, almost every lake known to contain the species also harbours the crustaceans *Mysis relicta* and *Pontoporeia affinis*. Ricker (1959) argues convincingly that these shrimplike species originated from arctic marine or brackish ancestors that were pushed in front of the advancing ice sheet; water was "sluiced up" from areas such as Hudson Bay and carried south, gradually freshening as it went. When the ice later retreated, proglacial lakes followed its receding front and deposited the "relicts" in their present locations. A similar origin has been postulated for European glacial relicts. If this dispersal system was effective for small crustaceans, which are poor swimmers, it may have been even more so for the *M. quadricornis* (which can and still does actively penetrate the lower courses of arctic rivers).

According to this theory, most mainland populations of this sculpin have been isolated from the sea since the onset of Wisconsin glaciation or even earlier. In contrast, fish in fresh water of Victoria Island probably originated from marine progenitors *since* the last ice recession (Johnson, 1964). Physical geography has precluded the formation of proglacial lakes on Victoria Island except in very restricted areas; on the other hand the modern lakes involved lie in or close to areas inundated by the sea *after* glacial retreat. The land later underwent a striking uplift; series of old beaches paralleling the present coastline are visible from the air. Sculpin populations in these lakes probably had a comparatively recent marine origin. Belief in separate colonization, from the sea, of mainland lakes and of arctic islands, is strengthened by the morphological divergence between marine and mainland forms and by the morphological intermediacy of the more recently evolved island forms.

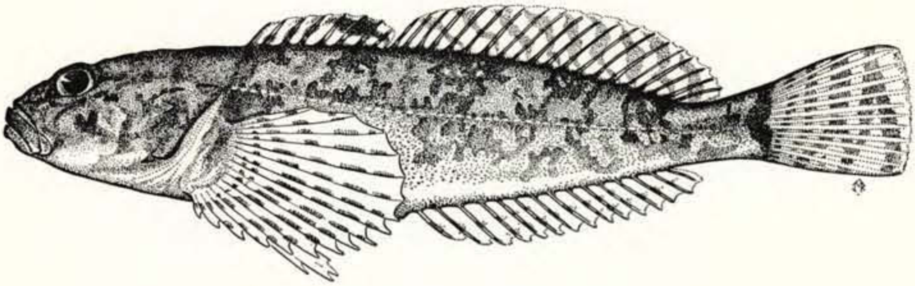
Biology

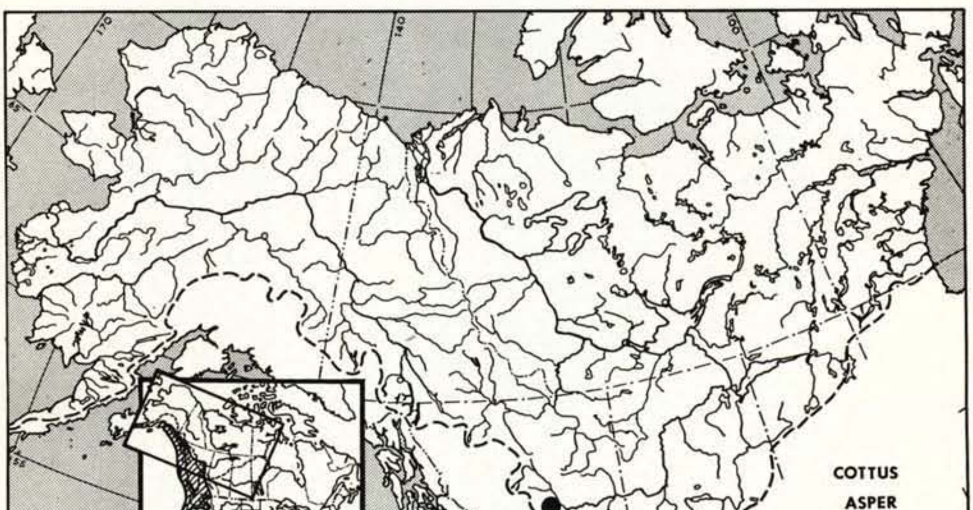
The deepwater sculpin occupies waters so deep that its presence in a lake is often known only through examination of stomachs of deep-feeding lake trout or burbot. In Great Bear Lake two lake trout netted at a depth of 400 m (1200 ft) contained deepwater sculpins (L. Johnson, personal communication). However, quite a few were taken in the same lake by trawling in water as shallow as 4–6 m (12–18 ft), almost invariably on a mud bottom. In Keller Lake, N.W.T., A. Peden (personal communication) concluded that they were probably all over the lake bottom, perhaps more concentrated in deep water during summer and moving inshore in autumn. In Great Slave Lake they have been collected at from 1 to 115 m, usually at 25–37 m (Rawson, 1951). In Wollastan Lake deepwater sculpins were in stomachs of lake trout netted at from 33 to 45 m (Rawson, 1959). One forms the impression that this diminutive fish may be quite abundant at great depths; in Great Bear they were often present in lake trout captured deep down where no other fish species occurred. In Keller Lake, Peden brought up a deepwater sculpin while sampling the deep bottom with an Ekman dredge!

Stomachs of deepwater sculpins taken from Great Bear Lake in 201–220 m contained adults and larvae of *Mysis*, copepods (*Limnocalanus*), and one sculpin was filled with chironomid larvae (L. Johnson, personal communication). In Lake Nipigon this species had eaten *Pontoporeia affinis* and chironomid larvae (Dymond, 1926) and Lake Ontario specimens contained these same items plus *Mysis relicta* (McAllister, 1961).

Little is recorded concerning their age or growth. In our area the largest reported specimen, which was from Great Slave Lake, measured only 69 mm standard length, in contrast to a 199-mm fish from Lake Ontario. The marine subspecies *M. q. quadricornis* grows as long as 365 mm in the USSR.

Spawning apparently occurs in summer. The sculpins found in lake trout stomachs from 1200 ft down in Great Bear Lake were taken in late July, and at that time their ovaries contained well-developed eggs. A Keller Lake female taken July 11 also had large eggs. Lake Ontario fish had nearly ripe eggs in early August. Nothing is known of the reproductive habits, but a male taken from Port Credit, Lake Ontario, in July 18, 1927, had a large clump of eggs in its mouth. Was this accidental, or does it signify parental care? At great depths, courtship and other social interactions must occur with little benefit of vision; this must be true in very deep fresh waters as well as in the abyss of the sea. The function of the elongate second dorsal fin in males is unknown. We have twice kept captive deepwater sculpins in aquaria for 2 weeks before they died; during this time they were timid and passive, refusing even live food. How this little fish lives, what its abundance is, and what role it plays in the ecosystem of deep northern lakes, are literally deep and dark secrets.





COTTUS
ASPER
MILES
0
400
KILOMETRES
0
600

PRICKLY SCULPIN

Cottus asper Richardson

Cottus is an old European name and *asper* means *rough.* The French common name for this species is *chabot piquant.*

Distinguishing Characters

The single chin pore, the well-developed palatine teeth, and the large number of anal rays.

Description

Body elongate, stout anteriorly and somewhat compressed posteriorly; head large, about one-third standard length; eye small, a little less than snout length. Mouth large; small teeth in both jaws and on the vomer and also on the palatines (Fig. 25). Large sharp spine at corner of preopercle, with one or two smaller ones hidden by the skin below it. Branchiostegal rays 6–6; the membranes of either side separated by the isthmus. Gill rakers short and stubby, usually 5 or 6. Two dorsal fins, the first with 7–10 spines and the second with 19–23 rays (in our area usually 19–21); 15–19 anal rays (usually 16–17 in our area); 15–18 pectoral rays; and 1 spine and 3–5 (usually 4) rays in the pelvic fins. No scales, prickling variable, restricted to a small area behind the pectoral fins or extending over most of the body; 32–43 pores in the complete lateral line. Vertebrae 34–29. Short pyloric caeca 4–6.

Size: To 300 mm (about 12 inches) in total length, but usually less than 150 mm (about 6 inches).

Sexual dimorphism: The genital papilla is long and V-shaped in males. In females it is short and round. Spawning males are darker than females.

Colour: Adults are a mottled dark brown to dark grey above and on the sides, and are white to yellow–white below. There are usually three oblique dark bands under the second dorsal fin. The rays of the dorsal, caudal, pectoral, and anal fins are usually barred. The 1st dorsal fin has a dark oval spot at its posterior end. The chin is usually lightly speckled. Males become dark during spawning season and both sexes develop a thin orange edge to the first dorsal fin during spawning season. Young specimens are similar to adults in colour, but are usually lighter and lack the barring on the fins.

Distribution

Pacific slope of North America: Ventura River, California, north to Seward (Kenai Peninsula), Alaska, and Queen Charlotte and Vancouver islands. The only populations known from east of the Continental Divide are in the upper Peace River (Mackenzie system).

Taxonomic Notes

The prickly sculpin was originally described as *Cottus asper* by Richardson in 1836 on the basis of specimens collected from the Columbia River by Gairdner. Synonyms are *Uranidea aspera, Trachidermus richardsoni*, and *Cottopsis parvus*; none of these names are commonly used in the modern literature. The record (Evermann and Goldsborough, 1907) of *Cottus gulosus* from southeastern Alaska is probably based on misidentified *C. asper*. Krejsa (1967) has reviewed the nomenclature history of the species.

There is considerable geographic variation in *Cottus asper*, particularly in the pattern and intensity of the prickling. R. J. Krejsa (personal communication) presents evidence that suggests *C. asper* is divisible into two genetically differentiated forms; one coastal and the other inland. These forms differ in their prickling pattern and migratory behaviour. However, in northern areas the coastal form has penetrated well inland and given rise to a form that approaches the inland form in prickling pattern. Krejsa refers to these northern inland populations as coastal derivatives. The populations in the upper Peace system are such coastal derivatives.

Postglacial Dispersal

The geographic range of *C. asper* includes a single possible glacial refuge, the Pacific. This species is widespread in the Columbia system and farther south in coastal areas. There were probably many isolated populations within the Pacific refuge. *Cottus asper* is euryhaline and probably attained its present northern distribution by northward postglacial dispersal from the Columbia system using both coastal and inland routes. The only populations in our area (upper Peace system) apparently crossed the Continental Divide into the Peace River from either the Fraser or Skeena rivers.

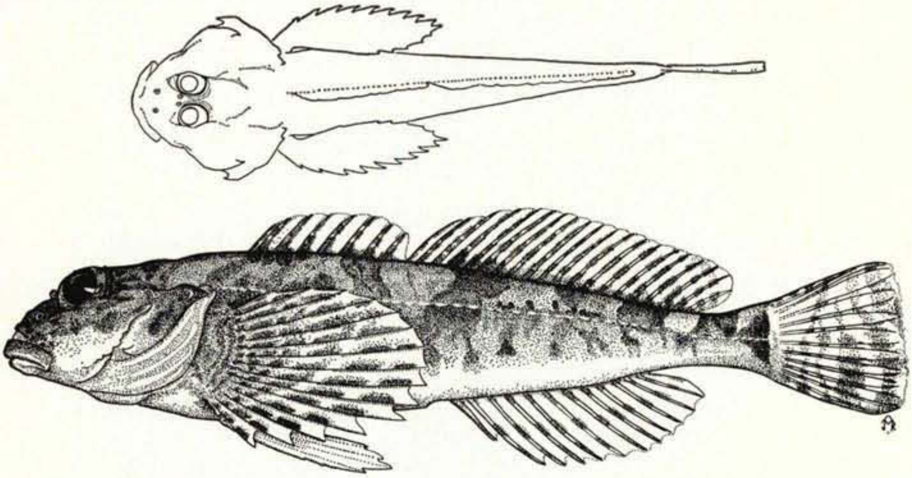
Biology

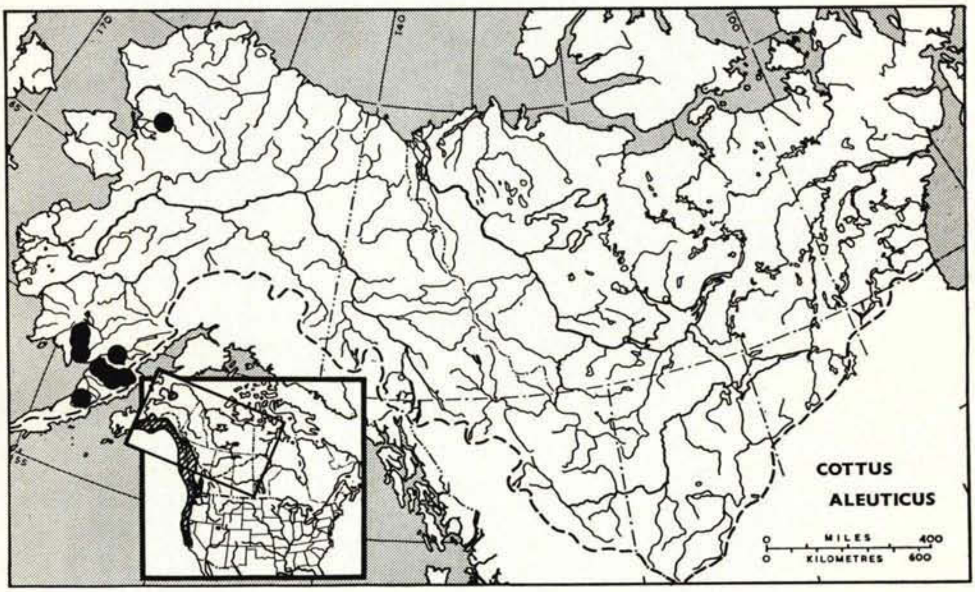
The prickly sculpin is typically an inhabitant of pools and quiet water areas in clear coastal rivers and streams. It avoids areas with high current velocites (G. D.

Taylor, personal communication). It may also be taken along lake shores and in turbid rivers. It is tolerant of salt water, and is often found in brackish areas. Coastal populations perform a downstream migration during breeding season, and spawning may occur in brackish water. Like most sculpins, *C. asper* is cryptic in its behaviour and seldom exposes itself during the day. Adults are usually solitary and may be territorial. The prickly sculpin feeds largely at night, when it moves into shallower water. The food is mainly aquatic insects and benthic invertebrates, but large individuals also consume small fishes. In the autumn salmon eggs are often found in *C. asper* stomachs. Nothing is known about the growth rate of *C. asper* in our area. Bond (MS, 1963) records a maximum age of 7 years in Oregon.

Spawning occurs in the early spring (mid-February to June). The eggs are laid in a nest, usually under a rock, and guarded and fanned by the male. Males may apparently spawn with more than one female, as over 25,000 eggs (in different stages of development) have been found in a single nest. The eggs are small (usually less than 1 mm in diameter) and orange in colour. They are usually found stuck to a rock that forms the roof of the nest. A large female may lay as many as 10,000 eggs, but single egg clusters are usually smaller than this. The young are 5–7 mm in total length, and begin swimming immediately upon hatching (R. J. Krejsa, personal communication). They are pelagic for 30–35 days before settling to the bottom; during the pelagic phase they tend to school (Northcote and Hartman, 1959).

Cottus asper is not used either for human or dog food, but may be of some importance as a forage fish for trout and char. It is an important item in the diet of mergansers.





170
140
100
65
55
COTTUS
ALEUTICUS
0 MILES 400
0 KILOMETRES 600

COASTRANGE SCULPIN

Cottus aleuticus Gilbert

Aleuticus means *of the Aleutians.* The French common name for this species is *chabot côtier.*

Distinguishing Characters

The single chin pore, absence of palatine teeth, rounded head, and complete lateral line.

Description

Body elongate, stout anteriorly and somewhat compressed posteriorly; head large, about one-third standard length; eye small, a little less than snout length. Mouth large; small teeth in both jaws and on the vomer. A single median pore under tip of lower jaw. A single sharp spine at corner of preopercle. Branchiostegals 6–6, the membranes of either side separated by the isthmus. Gill rakers short and stubby, usually 5–7. Two dorsal fins, the first with 8–10 spines and the second with 17–20 soft rays (in our area usually 19 or 20); 12–15 anal rays (usually 12 or 13 in our area); 13–16 pectoral rays (almost invariably 14 in our area); 1 spine and 4 rays in the pelvic fins. No scales, the prickles are restricted to a small area behind the pectoral fins; 34–44 pores in the complete lateral line. Vertebrae 34–38 (usually 36 or 37 in our area). Short pyloric caeca 3–6.

Size: To 115 mm (about 4.5 inches) in total length, but usually less than 100 mm (4 inches) long.

Sexual dimorphism: The genital papilla is longer in males than in females, and spawning males have a broad orange stripe on the edge of the first dorsal fin.

Colour: Adults are a mottled dark brown to light blue–grey above and on the sides, and white below. There are usually two or three oblique dark bars below the soft dorsal fin. The rays of the dorsal, caudal, pectoral, and anal fin are usually barred. The pelvic fins are usually immaculate but occasionally barred. The chin is usually heavily speckled. Young specimens (under 1.5 inches) are essentially coloured the same as adults, but usually lack the barring on the fin rays.

Distribution

Pacific coast of North America; continuously distributed in coastal streams and rivers from San Luis Obispo County, California, north to the Bristol Bay region, Alaska, and west in the Aleutian Island chain as far as Kiska; there is apparently a 500-mile range disjunction between Bristol Bay and an isolated population in the Kobuk River, a Chukchi Sea drainage in arctic Alaska. On Vancouver, Queen Charlotte, and Kodiak islands.

Taxonomic Notes

The coastrange sculpin was originally described from Kodiak Island by Lockington as *Uranidea microstoma* in 1880. However, Gilbert (1895) placed this species in the genus *Cottus,* and because the specific name *microstomus* was preoccupied in this genus he changed the name to *Cottus aleuticus.* The only synonym is *Cottus protrusus* described in 1933 by Schultz and Spoor from Unalaska Island.

There is some geographic variation in the number of anal fin rays in *Cottus aleuticus.* In the Bristol Bay region the commonest anal ray counts are 12 and 13 (counts of 14 are relatively rare), whereas *C. aleuticus* from southeastern Alaska and British Columbia rarely have 12 anal rays, and individuals with 14 anal rays are common. Populations from Kodiak Island and the Aleutian Islands are intermediate in this character.

Postglacial Dispersal

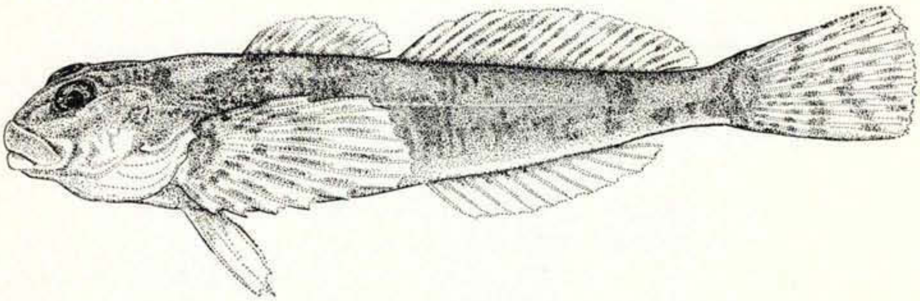
The distribution of the coastrange sculpin includes unglaciated regions in Alaska and also areas south of the maximum penetration of the Cordilleran ice sheet. This indicates that *C. aleuticus* may have survived glaciation in both areas. The disjunct (relict?) population in the Kobuk River and the pattern of geographic variation in anal fin ray numbers suggests that the *C. aleuticus* populations in our area probably survived glaciation in the Bering refuge. The populations of the coastrange sculpin in southeastern Alaska are probably the result of northward dispersal from the Columbia refuge. The morphologically intermediate populations on the Aleutian Islands and Kodiak Islands may be the result of a coming together of two forms (one dispersing south from the Bering refuge and the other dispersing north from the Columbia refuge). Alternatively, fin ray differences may be the result of direct phenotypic modification by the environment; even so the present pattern of distribution suggests dispersal from two sources.

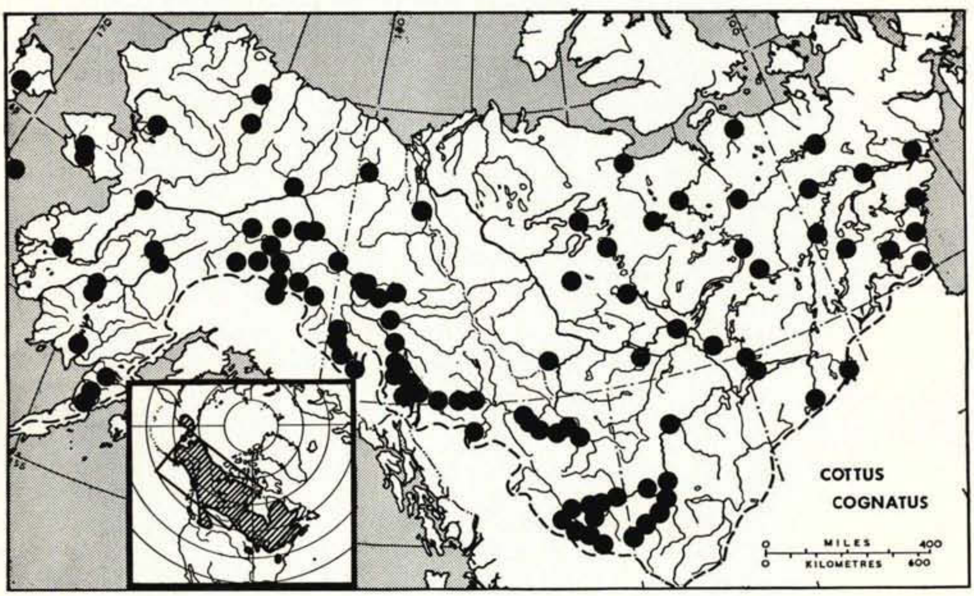
Biology

The coastrange sculpin is typically an inhabitant of swift riffle areas in coastal streams and rivers. It is apparently tolerant of brackish water and is occasionally found in estuaries. In the Bristol Bay region *C. aleuticus* is often taken in quiet water along lake shores or in still areas near the mouths of creeks entering lakes. Under such circumstances *C. aleuticus* may be found on sand or even mud bottoms. In streams and rivers it is usually associated with a coarse gravel substrate (G. D. Taylor, personal communication). *Cottus aleuticus* is cryptic, usually solitary, and may be territorial, although Greenbank (1957) recorded a daylight aggregation of this species. The coastrange sculpin feeds largely at night, mainly on aquatic insects and benthic invertebrates (particularly molluscs), but in the autumn the coastrange sculpin feeds extensively on salmon eggs. Most of this consumption is probably stray eggs. In the spring adult *C. aleuticus* may also feed on migrating pink and chum salmon fry. Nothing is recorded on the growth rate and age of *C. aleuticus* in our area. Bond (MS, 1963) records a maximum age of 4 years in Oregon.

Spawning occurs in the early spring (mid-February to June) and in our area appears to reach a peak in late May. The eggs are usually laid under a rock. Males apparently spawn with more than one female, as over 7000 eggs (in different stages of development) have been found in a single nest. The eggs are adhesive, small (usually less than 1.5 mm in diameter), and orange in colour. A large female may lay as many as 800 eggs, but usually single egg clusters are smaller than this. The young are planktonic, and in streams they tend to congregate in pools and areas of slow water. They do not show a marked preference for currents until they reach a size of about 60 mm (G. D. Taylor, personal communication), but they become benthic at a much smaller size. In the large Bristol Bay lakes planktonic *C. aleuticus* larvae are found near the surface even over deep water (Heard, 1965). In these lakes the planktonic larvae are eaten by young sockeye salmon.

Cottus aleuticus is not used either for human or dog food, but may be of some importance as a forage fish for trout, char, and young salmon, and as a predator on salmonid eggs and the fry of pink and chum salmon.




COTTUS
COGNATUS
MILES
400
KILOMETRES
600

SLIMY SCULPIN

Cottus cognatus Richardson

Cognatus means *related* (to the European species). The French common name for this species is *chabot visqueux*.

Distinguishing Characters

The double chin pores, incomplete lateral line, and low number of dorsal and anal rays.

Description

Body elongate, stout anteriorly and compressed posteriorly; head moderate, about one-third to one-quarter standard length; eye small, a little less than the snout length. Mouth large; small teeth in both jaws and on the vomer. Two pores close together under tip of lower jaw (Fig. 24A). One, two, or three spines on preopercle. Branchiostegals 6–6. Gill rakers short and stubby, usually 4 or 5. Two dorsal fins, the first with 7–9 (rarely 10) spines and the second with 14–19 rays (usually 14–16 in our area); 10–13 anal rays (usually 10 or 11 in our area). The last two dorsal rays, and sometimes the last two anal rays, arise from separate bases in some individuals of *C. cognatus* (unlike all other species of *Cottus* in our area, in which the last pair of rays in each of these fins share a common base). Pectoral fin with 12–15 rays; pelvic fins with 1 spine and with 3 rays, or with 4 rays, the fourth usually short. No scales; prickles weak, restricted to a small area behind the pectoral fins; lateral line incomplete, ending under the second dorsal fin with 12–26 pores. Vertebrae 33–35. Short pyloric caeca 2–5.

Size: To 120 mm (4.7 inches).

Sexual dimorphism: The genital papilla is about twice as long in males as in females. Spawning males have a black first dorsal fin with an orange edge.

Colour: Adults are a mottled light brown to dark grey above and on the sides, and whitish (occasionally orange) below. There are usually two or three oblique dark bars below the soft dorsal fin. The rays of the dorsal, caudal, and pectoral fins are usually barred. The pelvic and anal fins are usually immaculate but occasionally barred. The chin is usually lightly speckled. During spawning season males become notably darker.

Distribution

In eastern Siberia, in the Anadyr River and on the Chukotsk Peninsula. On St. Lawrence Island in Bering Sea. In North America, in most Bering Sea drainages, and Arctic Ocean drainages east to Ungava Bay and Labrador. In the south, from Nova Scotia to Virginia, the Great Lakes basin, isolated populations in Iowa, most of Manitoba, and northern portions of Saskatchewan and Alberta. On the Pacific coast, in the upper but not lower portions of the Columbia and Fraser rivers, and in northern coastal drainages including the Stikine, Taku, Chilkat, Alsek, Copper, and Susitna rivers, and on Kenai Peninsula. (The report of this species from Martin River, Ocean Falls, B.C. (McAllister and Lindsey, 1961) is erroneous, based on a museum labelling mistake.) In our area, generally distributed on the mainland, but not recorded from islands (except St. Lawrence) nor the mainstem Mackenzie River.

Taxonomic Notes

Cottus cognatus was named by Richardson in 1836 from Great Bear Lake. *Cottus gracilis* from New York, *C. philonips* from Kicking Horse River, B.C., *C. chamberlaini* from Loring, Alaska, and *C. kaganowskii* from Anadyr River, USSR, are probably all this species (McAllister and Lindsey, 1961).

In slimy sculpins, geographic variation in morphology gives a particularly strong indication of dispersal from more than one glacial refuge. Most specimens from Alaska have a double fin ray on the last anal fin basal, and four rays in the pelvic fins (although the fourth may be reduced). This "northern type" extends into all Pacific drainages as far south as the Stikine River, and into upper Yukon River, the Liard River, and in the Peace River in Alberta. In contrast a "southern type," commonly with a single last anal ray and only three pelvic fin rays, occupies the Great Lakes – St. Lawrence basin, Quebec, and most drainages entering the west side of Hudson Bay north to about Chesterfield Inlet. In northern Canada these "pure northern" and "pure southern" forms are separated by a wide band of populations resembling the northern form with respect to the split anal fin ray, but intermediate with respect to frequency of pelvic ray counts. A few populations at the northern border of the "southern type" show other conditions of intermediacy. Finally, in the Columbia, Fraser, and upper Peace rivers in British Columbia occur populations that are intermediate with respect to both characters.

The case for recognition of subspecies is marginal. It is possible to combine frequencies of the two characters discussed in such a way as to separate about 80% of the populations studied into northern-source or southern-source types (McAllister and Lindsey, 1961). However, this separation is of populations, not individuals. If the differences have actually arisen during long isolation, further investigation may reveal additional characters that will permit clearer identification. Until then, we think it better to omit subspecific names.

Postglacial Dispersal

The northern form probably survived glaciation in the Bering area. Its presence on St. Lawrence Island, as well as in eastern Siberia and western Alaska, shows that it occupied the Bering land bridge, since it apparently does not take to salt water, and has failed to invade other islands postglacially. (It has, however, been recorded from brackish water in Ungava Bay by Dunbar and Hildebrand (1952).) From there it spread south along Pacific coastal drainages as far as the Stikine, capitalizing on its tendency to occupy the type of stream likely to be involved in headwater interchanges. It also spread eastward into the Liard and lower Peace. The southern form, arising from one or more refuges in the southeast, followed glacial retreat northeast to Ungava, and also northwest. It probably entered what are now headwaters of the Mackenzie, and in spreading downstream met and interbred with the northern form; populations carrying a mixture of genes from both sources spread eastward across the Barrens.

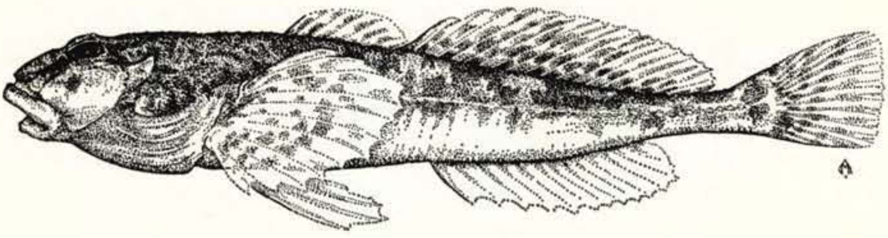
This tidy explanation ignores the British Columbia populations, which are intermediate in both characters. Within the Peace River, a gradient exists, with completely intermediate populations above the Peace River canyon, completely "northern" types in Alberta, and intergradation between. It is difficult to postulate a convincing sequence of postglacial events that would allow postglacial hybridization between "northern" (Alaskan) and "southern" (Great Lakes?) forms leading to invasion by these hybrids of the upper Peace, the Fraser, and the Columbia. Perhaps a third refuge existed west of the Continental Divide in Washington State, where a form evolved that is superficially intermediate between the other two. Perhaps this form arose from hybridization during the pre-Wisconsin interglacial period, as suggested in "Zoographic Patterns." Another problem concerns the apparent absence of this fish from the whole mainstem of the Mackenzie River. The species presents excellent material for further study.

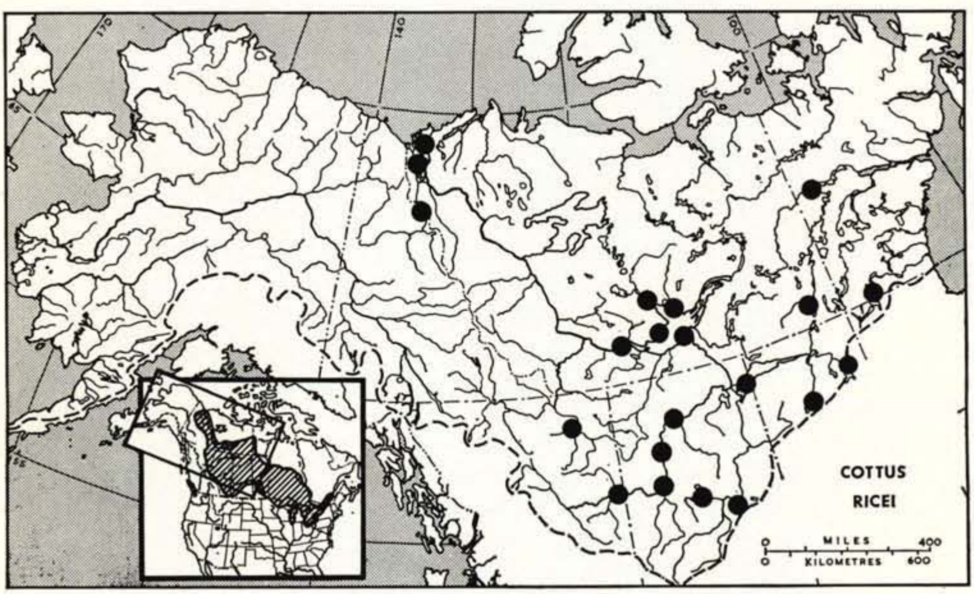
Biology

The slimy sculpin is widespread in rivers and streams of the north, as is evident from examination of the distribution map; locality records form chains along some roads, where every bridge and culvert harbours the species. It is less typical of lakes than of cool running water with rocky or sandy bottom. It is evidently better adapted to subarctic conditions than any other species of *Cottus*. L. Johnson (personal communication) found in Great Bear Lake that the slimy sculpin was more typical of rocky bottoms than was the deepwater sculpin, which favoured mud. The former was taken only in the shallower parts of the lake. Similarly A. Peden (personal communication) reported that in Keller Lake, N.W.T., slimy sculpins were usually in rocky areas subject to some current or wind action, and apparently did not occur in waters over 10 m (30 ft) deep. In both lakes some slimy sculpins were found in lake trout stomachs, but never from great depth. In contrast, in Lake Superior the species was most abundant at depths greater than 80 m (240 ft) (Dryer, 1966).

Regarding spawning season, Richardson (1836) wrote that he took the species "in considerable numbers in the clear waters of Great Bear Lake during the month of May, at which period it resorts to the stony shallows to spawn . . . some individuals, . . . which are full of roe, measure only two and a half inches of total length."

Farther south it typically spawns in running water; the eggs are attached to the underside of stones and guarded by the males. The dark body colour of the male and orange-trimmed dorsal fin at this time probably serve for sexual recognition and for warning, but little has been described of their reproductive habits. Similarly feeding has been described only in general terms; principal food items are said to be aquatic insects, crustaceans, small fishes, and aquatic vegetation. Almost nothing seems to be known of the growth and life history of this wide-ranging species.




COTTUS
RICEI
0 MILES 400
0 KILOMETRES 600

SPOONHEAD SCULPIN

Cottus ricei (Nelson)

Ricei is named after the discoverer F. L. Rice. The French common name for this species is *chabot à tête plate*.

Distinguishing Characters

The very wide flat head with relatively long, curved, preopercular spines, the single chin pore, and the usually dense prickling on the body.

Description

Body elongate, stout anteriorly and compressed posteriorly; head moderate, usually a little more than one-third standard length. In dorsal view, the region ahead of each eye projects forward almost as far as the tip of the snout, giving the border of the head behind the lip a "W" shape. The skin on the chin is wrinkled. Eye small, usually less than snout length. Mouth small for a sculpin; small teeth in both jaws and on the vomer. A single median pore under tip of lower jaw. Three, sometimes two or four, preopercular spines, the uppermost long (about two-thirds the eye diameter) curved inward and resembling a bison's horn. Branchiostegals 6–6, the membranes of either side separated by the isthmus. Gill rakers short and stubby, 4–6. Two dorsal fins, the first with 7–10 spines and the second with 16–18 soft rays; 12–13 anal rays; 14–16 pectoral rays; and 1 spine and 4 rays in the pelvic fins. No scales, the prickles are usually well developed and in our area often cover the whole body; 33–36 in the complete lateral line. Sensory pores on head large. Vertebrae 34–38. Short pyloric caeca 4–6.

Size: Rarely up to 107 mm (4.2 inches), usually less than 75 mm.

Sexual dimorphism: In adults the genital papilla is a short, broad triangle in males, and much reduced in females.

Colour: Light brown above and white below. There are usually darker bars on the back and sides. The rays of the dorsal, caudal, and pectoral fins are usually barred; the rays of the pelvic and anal fins are usually immaculate. The chin is lightly speckled. Young specimens are coloured essentially the same as adults, but usually the barring on the fin rays is absent.

Distribution

Confined to Canada and the Great Lakes basin. Throughout much of the Mackenzie River basin, but not reported above the canyon on the Peace River, nor above the Grand Canyon of the Liard. Otherwise present in tributaries to the west sides of Hudson and James bays, in each of the Great Lakes, in the St. Lawrence River downstream as far as Ile d'Orleans, and in Nipigon and Lake Charlevoix in Michigan. Ryder et al. (1964) found it in marine waters of James Bay off Akimiski Island, and in island tide pools, but surface salinities are relatively low in this area.

Taxonomic Notes

Cottus ricei was described from Lake Michigan by Nelson in 1876. It is a very distinctive sculpin with an unconfused taxonomy. Perhaps its closest relative is one of the Old World sculpins, *Cottus sibiricus, C. spinulosus,* or *C. gobio* (McAllister and Lindsey, 1961).

Postglacial Dispersal

The spoonhead sculpin probably survived glaciation in the upper Mississippi basin, despite its absence from there now. It moved northward in the wake of the retreating ice, and apparently died out in the southern portion of its original range. During ice recession it may have gained access to the temporary Lake Barlow-Ojibway that lay north of the present height of land between the Great Lakes and James Bay; Lake Barlow-Ojibway extended east to Lake Abitibi, where the species now occurs. Its tolerance of brackish water is evidenced by its occurrence around Akimiski Island, but this has not enabled it to extend its range along the arctic coast away from the Mackenzie delta, nor up the east side of Hudson Bay. In fact the distribution of this species is unique, and the factors governing its dispersal are unknown.

Biology

Most northern collections of spoonhead sculpins are from the shallows of large muddy rivers; a few are from lakes, and, in James Bay, from tide pools. In contrast, at the southern end of their range in the Great Lakes they may occupy deep water, down at least to 200 mm (600 ft); they are not found in tributary streams, but have been taken from the St. Lawrence River. Despite this diversity of habitat, they are not known to be strikingly abundant or successful anywhere, and their range, although quite wide, seems curiously bounded. They may perhaps be common in the depths of big turbid rivers, where there has been little sampling. The young are sometimes taken in the shallows of such rivers, and larger individuals may be seined at the outer limit of safe wading depth (or, frequently, just beyond). Their extremely flattened heads, large head pores, small eyes, and dense armour of prickles would seem to adapt them well to such an environment. But, if deeper waters of turbid rivers are their preferred habitat, it is difficult to understand why they are absent from the rivers of the Great Plains of the United States, where they presumably originated. In the south their food is said to consist principally of plankton and aquatic insects. They are eaten by lake trout and by burbot, but in the north what they themselves eat has not been studied. Their spawning season is probably spring, but nobody knows.

THE PERCHES — Family PERCIDAE

Perches have a spiny first dorsal fin, separated by a space from the second soft-rayed dorsal fin. The anal fin has one or two spines, the gill cover ends in a flat spine, and the scales are ctenoid (having spiny serrations). Some, like the walleye, grow large; eastern North America also contains dozens of small species, which are called darters. All members of the family are freshwater, mostly American but some range across temperate Eurasia. Of roughly 120 species, only 3 enter our area.

KEY TO THE SPECIES

1(6) Snout longer than eye; tail forked; edge of preopercle serrated 2

2(3) No large canine teeth in jaws (Fig. 26A); anal fin with 2 spines and 6–8 soft rays; pelvic fins close together .... American yellow perch, *Perca fluviatilis flavescens* .... (Mitchill) (p. 343)

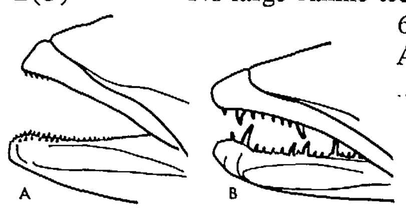


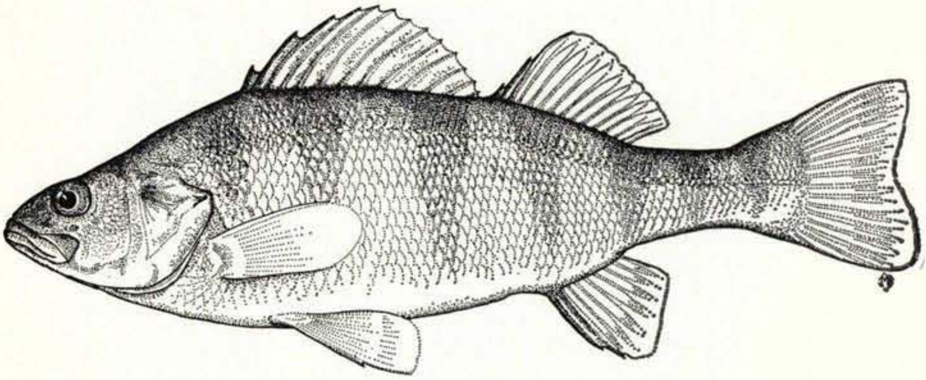
Fig. 26. Jaws and teeth: A, *Perca fluviatilis*; B, *Stizostedion vitreum*.

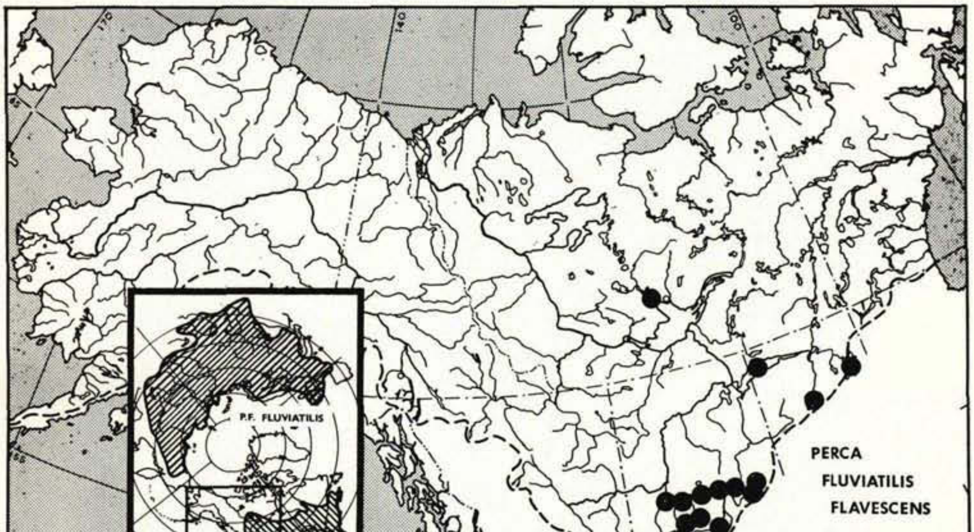
3(2) Strong canine teeth in upper and lower jaws and on the roof of the mouth (Fig. 26B); anal fin with 2 weak spines and 11–14 soft rays; pelvic fins widely separated (interspace equal to breadth of fin base) 4

4(5) Spinous dorsal with a large black blotch at back, otherwise with obscure dusky mottlings but without rows of round black spots, lower lobe of caudal usually with a milk-white tip; soft dorsal rays usually 20–22 (rarely 18 or 19); pyloric caeca 3 .... Yellow walleye, *Stizostedion vitreum vitreum* (Mitchill) (p. 347)

5(4) Spinous dorsal without a prominent black blotch at posterior end, but with rows of round black spots (not evident in young); lower lobe of caudal usually not tipped with white; soft dorsal rays 17–20; pyloric caeca 5–9 .... Sauger, *Stizostedion canadense* (Smith)
A slender, cylindrical fish not reported from our area but occurring in the Red Deer and other tributaries of the Saskatchewan River system.

6(1) Snout shorter than eye; tail not forked; edge of preopercle smooth; length not over 5 cm (2 inches) .... Iowa darter, *Etheostoma exile* (Girard) (p. 351)




P.F. FLUVIATILIS
P.F. FLAVESCENS
PERCA
FLUVIATILIS
FLAVESCENS
MILES
0
400
KILOMETRES
0
600

AMERICAN YELLOW PERCH

Perca fluviatilis flavescens (Mitchill)

Perca is the ancient name of the perch meaning "dusky"; *fluviatilis* means *of the river*; and *flavescens* means *yellowish*. The French common name for this species is *perchaude*.

Distinguishing Characters

The two separate dorsal fins, no canine teeth, and the distinct, dark, vertical bars on the sides.

Description

Body much deeper than wide, the depth about 3.5 in standard length, compressed; head large, more than one-quarter total length; eye moderate, smaller than snout; snout blunt. Mouth terminal, oblique; no large (canine) teeth (Fig. 26A), but numerous small teeth on the premaxillary, dentary, head of vomer, and palatines; no teeth on maxillary, tongue, or basibranchials. Branchiostegals 7 + 7; gill membranes separate; gill rakers short, 3–5 + 15–16. Preopercle and shoulder girdle serrated, the preopercular serrations with forward-directed hooks below; opercle with a single spine. Dorsal fins separated, the first with 13–15 spines, and the second with 2 or 3 spines and 13–15 soft rays; anal fin with 2 spines and 7 or 8 soft rays; 13–15 pectoral rays; pelvic with 1 spine and 4 or 5 soft rays. Pelvic fins close, separated by less than the breadth of the fin base. Scales large, ctenoid, 55–60 pored scales in lateral line in our area (54–70 elsewhere). Vertebrae 40–41 (39–42 elsewhere). Short pyloric caeca 3–5.

Size: Length usually less than 35 cm (14 inches) and weight 0.4 kg (1 lb); in the south recorded up to 53 cm (21 inches) and weight 1.9 kg (4 lb).

Sexual dimorphism: No obvious external differences between the sexes except colour at spawning time. In many populations mature females are larger than mature males. The pelvic fins of males are often longer than those of similar sized females.

Colour: In adults the back is olive green to brown, the sides are yellowish with 6–8 dark vertical crossbars, underparts pale. Dorsal fins dusky, often with a dark spot at the posterior base of the first dorsal fin. Pectoral and pelvic fins yellowish, or reddish-orange in breeding males.

Distribution

The species ranges in Eurasia from the British Isles eastward through most of Europe and in Arctic Ocean tributaries of the USSR east to the Kolyma River.

The natural range of the North American subspecies extends from the upper Mackenzie River basin through Hudson Bay drainages east to Nova Scotia, and south on the Atlantic coast to South Carolina; throughout the Great Lakes, and in the upper Mississippi system south to northern Missouri. Widely introduced elsewhere. In our area yellow perch occur in many lakes in central Alberta but are rare northwards; our northern-most locality is Great Slave Lake where we took two small specimens from Rae Arm.

Taxonomic Notes

Linnaeus named the European yellow perch *Perca fluviatilis* in 1758. The North American form was named *Perca americana* by Schranck in 1792, but this name had already been applied earlier to the white perch; the next available name for the yellow perch was *Morone flavescens*, applied by Mitchill in 1814. Svetovidov and Dorofeeva (1963) have compared specimens from the Old and New worlds, and conclude that (in addition to a species *Perca schrenki* from Lake Balkhash) there is a single circumpolar species with three subspecies. Compared with the American form, the European has a wider skull and higher supraoccipital crest. Because the European form was named earlier, the North American yellow perch, which has usually been referred to as a distinct species, *Perca flavescens*, should properly be called *Perca fluviatilis flavescens*. The European subspecies is *Perca fluviatilis fluviatilis*. An intermediate form occurs in the Kolyma River basin of Siberia.

Postglacial Dispersal

The yellow perch was probably distributed continuously across northern Eurasia and North America some time prior to Wisconsin glaciation. Fossil bones, not distinguishable from the contemporary *P. fluviatilis*, have been found in Quaternary deposits east of the present Siberian range of the species, on the Kyrchak Peninsula, Chaunskaya Gulf (Svetovidov and Dorofeeva, 1963). During the last or an earlier glaciation the range became discontinuous in the Bering region, and has not since been reunited.

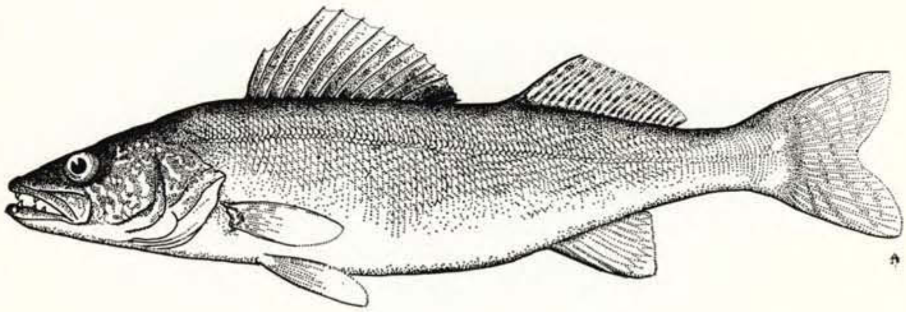
In North America, yellow perch probably survived south of Wisconsin glaciation in the upper Mississippi basin, as well as farther east, but not in the upper Missouri.

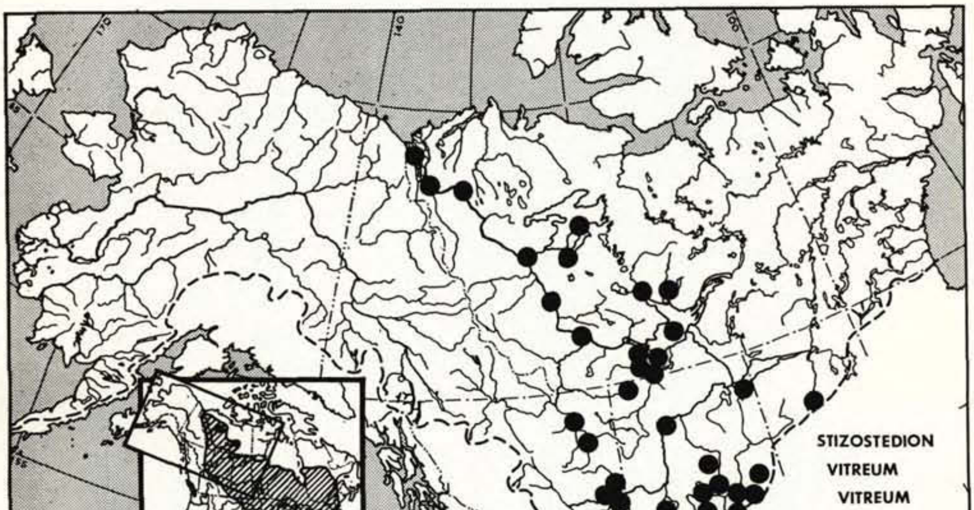
Bailey and Allum (1962) believe that perch moved westward postglacially into the middle Missouri basin from either the Minnesota or the Des Moines basin. However, Metcalfe (1966) cites fossil evidence that "it ranged far to the south in the Great Plains in Illinoian (?) time. That subsequently it was extirpated in the western Plains suggests occurrence of a period or periods of marked aridity there, possibly in Sangamonian or in post-glacial time." Northward extent of the yellow perch is apparently limited by temperature; only one Ontario collection has come from north of the 60 F July isotherm (Ryder et al., 1964), and yellow perch abundance drops off rapidly towards the north in the Mackenzie basin.

Biology

Yellow perch are usually found in quiet bays or in sluggish streams. They frequently travel in schools in or near weedy areas, sometimes making inshore migrations at dusk. Perch eat small fish of other species and their own, as well as crustaceans, molluscs, and insect larvae. Growth is slow; in Lake Manitoba 3-year-old fish are 12.7 cm (5.0 inches) long and weigh 28 g (1 oz); 8-year-olds are 27.4 cm (10.8 inches) and weigh 312 g (11 oz). Sexual maturity may be reached at 2 years of age. Spawning occurs in April, May, or possibly later. In shallow water, eggs are expelled in ropelike strands bound in a gelatinous sheath. Some of these thin ribbons of eggs are 2 m or more in length; a large female may produce 40,000 eggs. Eggs are usually tangled in the stems of water plants; some may drift free after a violent storm and be cast up on beaches. Eggs hatch in about 3 weeks.

Although perch are small, they have firm white flesh and are delicious to eat. Over $1.5 million worth of yellow perch was marketed in Canada in 1962, some coming from a number of central Albertan lakes in the upper Mackenzie drainage. Yellow perch are also a favourite among anglers in many Albertan lakes, being quite easy to catch, beautiful to look at, and producing convenient pan-sized fillets.




STIZOSTEDION
VITREUM
VITREUM
MILES
400
KILOMETRES
600

YELLOW WALLEYE

Stizostedion vitreum vitreum (Mitchill)

Stizostedion means *pungent throat* and *vitreum* means *glassy* (from the large milky eye). The French common name for this species is *doré jaune.*

Distinguishing Characters

The two separate dorsal fins, and the large mouth with canine teeth.

Description

Somewhat rounded, the depth about 4.5 in standard length; head large, more than one-quarter total length; eye moderate, less than snout; snout pointed. Mouth large, terminal; well-developed canine teeth on the premaxillary and dentary (Fig. 26B) and on the palatines and the head of vomer; no teeth on maxillary, tongue, or basibranchials. Branchiostegals 6–8 + 7–8; gill membrances separate; gill rakers short, 4–5 + 12–15. Preopercle serrated, the points of the lower serrations turned forward; opercle with one or more spines. Dorsal fins separated, the first with 12–16 spines, and the second with 1 spine and 17–22 soft rays (usually 20–22); anal with 2 weak spines and 12–14 rays; 15–16 pectoral rays; pelvics with 1 spine and 5 soft rays. Pelvic fin bases separated by a space about the width of one fin base. Scales small, ctenoid, 93–108 pored scales in the lateral line in our area (as few as 83 elsewhere). Cheeks and upper surface of head nearly naked. Vertebrae 46–48 (43–50 elsewhere). Long pyloric caeca, 3, often but not always as long as stomach.

Size: In our area length to 78 cm (30 inches) and weight to 5 kg (11 lb); reportedly to 25 lb in the south.

Sexual dimorphism: Average size of mature females larger than males. White patch on lower caudal lobe more pronounced in males.

Colour: In adults the back is dark green to brown, often with brassy yellow specks, the sides are mottled yellowish, and the underparts are white. The spinous dorsal is dusky with a black patch at its posterior base; soft dorsal and caudal speckled with dark spots; the ventral lobe of caudal fin usually with a creamy white patch. The sides of the head are vermiculated. Cornea of eye slightly milky, giving fish its "wall-eyed" appearance. Young specimens (to 30 cm or 12 inches) with irregular dark blotches on the sides.

Distribution

Mackenzie River system; Hudson and James Bay drainages from the Churchill to the Fort George rivers; east in Quebec to the Manicouagan River; absent from New Brunswick; south on the Atlantic coast of North Carolina; in the Mississippi basin south as far as Georgia.

In our area, throughout most of the Mackenzie River basin north to Arctic Red River; not ascending the Peace River above the Peace Canyon, nor the Liard above the Liard Canyon.

Taxonomic Notes

There are three Eurasian and two North American species in this genus. European species have usually been called *Lucioperca,* but Svetovidov and Dorofeeva (1963) showed that they do not differ sufficiently from North American species to warrant a different genus. The name *Stizostedion* was proposed by Rafinesque in 1820, whereas *Lucioperca* was not used in a proper binomial name until 1822. Therefore all the Eurasian as well as North American species should be placed in the genus *Stizostedion.*

The walleye was first described as *Perca vitrea* from Cayuga Lake, New York, by Mitchill in 1818. It has also been called *Lucioperca americana* and *Perca salmonea.*

We refer to our fish as "yellow walleye," subspecies *Stizostedion vitreum vitreum* (Mitchill), to distinguish it from the "blue walleye," *Stizostedion vitreum glaucum* Hubbs of Lake Erie. Differences are in colour, and size and spacing of the eyes. Hubbs and Lagler (1958) wrote "The 'blue pikes' of Lake Ontario, of lakes in the St. Lawrence River and Lake Huron drainages in Ontario and of Lake Winnipeg in Manitoba have been identified with this subspecies but they are probably not quite identical. They need further study."

Postglacial Dispersal

Walleyes are apparently not native to the upper Missouri system. During deglaciation they probably spread north from the upper Mississippi system into Lake Agassiz II by way of the Warren River outlet, and from there north into the Mackenzie system.

Biology

The centre of abundance of walleyes is to the south of our area. In the warmer lakes at the southern end of the Mackenzie basin walleyes may be fairly numerous. In

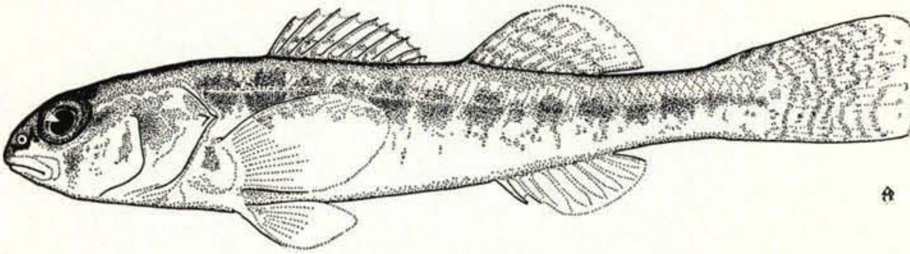
Great Slave Lake they are confined to certain shore areas, although common in small tributary lakes and rivers; in Great Bear Lake they are largely restricted to the mouth of the Johnny Hoe River. In the main stem of the Mackenzie River walleyes are probably more abundant in the warmer southern reaches such as the Peace than at its northern extremity. Although they are said to prefer deep water in summer in more southern lakes, most walleyes in Great Slave Lake are caught in depths of less than 5 m (15 ft) and none below 10 m (30 ft).

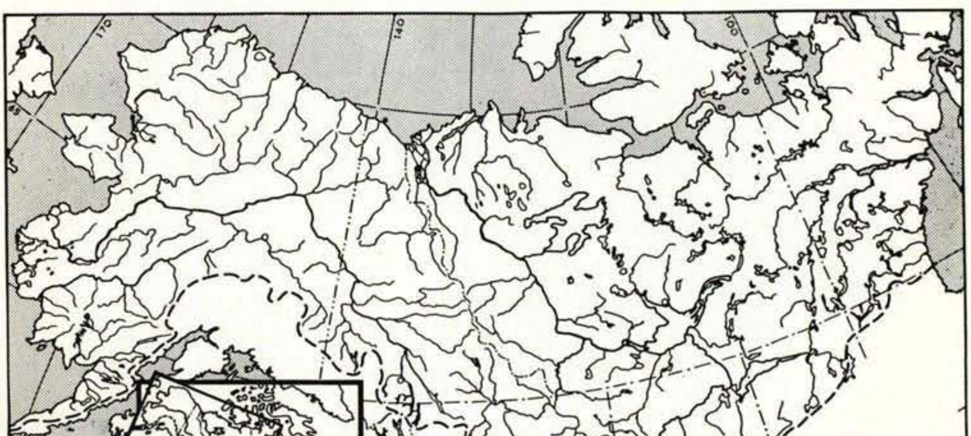
Walleyes are largely fish eaters. Digestion may be rapid or else feeding sporadic, for most studies have shown a large proportion of walleye stomachs to be empty. In Great Slave Lake the diet is reported to be three-quarters fish (suckers, sticklebacks, cottids, and whitefish, in decreasing order of abundance), and the rest chiefly mayfly nymphs, other aquatic insects, and amphipods. In Lake Athabasca walleyes fed mainly on trout-perch and ninespine sticklebacks, with occasional minnows, whitefish, goldeyes, and ciscoes.

Growth is much slower in northern than in southern waters. In Iowa a walleye at 5 years of age may attain 48 cm fork length. A 5-year-old fish in Cree Lake, northern Saskatchewan, is only about 41 cm long (31 oz); a 5-year-old fish in Great Slave Lake is only 20 cm long (4 oz). Maximum recorded ages of walleyes are 9 years in Cree Lake and 14 years in Great Slave. In Great Bear Lake, close to their northern limit, walleyes are very slow growing and long living; fish 16 years old and only 1.8 kg (4 lb) weight are not uncommon.

In Manitoba female walleyes are said to mature at age 6, males a year earlier; in southerly areas maturity comes at an earlier age. Walleyes spawn in spring just before or after the ice leaves. Males migrate first to the spawning grounds, which are either sandy or rocky shoals in lakes, or gravel shallows in streams. Egg laying, described by Ellis and Giles (1965), occurs mostly in late evening. One female is accompanied by one or more of the generally smaller males. Spawning is sometimes accompanied by vigorous milling and splashing. One female deposits from 35,000 to 600,000 small eggs (about 2 mm diameter), which are abandoned. Hatching occurs in from 12 to 18 days or more, depending on water temperatures.

The yellow walleye is prized as a food fish, its meat being firm, flaky, and white, quite dry, and bone-free. In 1962 the total commercial catch of walleyes in Canada had a market value of over $5 million, only slightly less than that for whitefish. Much of this came from prairie lakes and the Great Lakes, but some of the lakes in the southern Mackenzie basin such as Kakisa, Tathlina, Lesser Slave, and La Biche produce important poundages of walleyes. Walleyes are also attractive to anglers; in addition to their excellent eating qualities, they have migratory habits that sometimes make their detection difficult for the angler. In different areas yellow walleyes are also known as walleyed pike, pickerel, yellow pickerel, pikeperch, or doré.





170
140
100
ETHEOSTOMA
EXILE
MILES
400
KILOMETRES
600

IOWA DARTER

Etheostoma exile (Girard)

Etheostoma is stated by Rafinesque to mean *"various mouths,"* but derivation is obscure; *exile* means *slim*. The French common name for this species is *dard à ventre jaune*.

Distinguishing Characters

A slender little spiny-rayed fish with smooth preopercle, short snout, and unforked tail.

Description

Body slim, greatest depth about 6 in total length; head about one-quarter standard length; snout short, decurved, eye about 1.2 times snout length; upper lip slightly overhanging tip of lower jaw. Maxilla reaching under anterior one-half of pupil; teeth on premaxilla, dentary, vomer, palatines, and basibranchials. Branchiostegals 6 + 6; gill membranes united at front. Gill rakers soft and feeble, about 10 or 11 (2–3 + 8–9). Edge of preopercle smooth. Dorsal fins separated, the first with 8–10 spines, the second with 10 or 11 rays; anal with 2 spines and 6–8 rays; 13 or 14 pectoral rays; pelvic with 1 spine and 5 rays. Outline of caudal fin somewhat rounded, not forked. Scales ctenoid, 54–63 along side, the pored lateral line with 9–30 pored scales (none on small specimens), often with 1 or 2 scales without pores before the last pored scale. Scales present on opercle and subopercle, but no scales on nape of neck ahead of first dorsal, nor on breast; cheek behind eye naked or with a very few scales. (Scalation is very variable; the foregoing description applies to fish in our area). Vertebrae 34–40 (about 38 or 39 in our area). Short pyloric caeca 3.

Size: To about 5 cm (2 inches).

Sexual dimorphism: Males at breeding time brilliant, the first dorsal with an orange–red band, with dark purplish or green above and below; underparts yellow, lower fins red–brown with some green; alternating reddish and either blue or green bars on sides. Females paler and less vivid. The first dorsal and anal fins are larger in males than females. Females are larger than males, and have an elongate tubelike genital papilla.

Colour: Upper parts and sides light green, finely blotched with dark brown. About nine dark brown patches along sides, sometimes alternating with rusty red. Belly pale yellowish; an orange band between base of pectoral and anal fins. Distinct dark tapering vertical bar below the eye that has been described as a "tear drop," dorsal and caudal fins with dark speckling; pectorals, pelvics, and anal pale and unmottled. First dorsal may have row of dark brown patches near base, and sometimes a narrow dark border to outer margin. Breeding colours described under "sexual dimorphism."

Distribution

From Alberta through the upper Churchill and the Saskatchewan river systems, the Severn, Attawapiskat, and Albany river systems, east to Lake Champlain, south to Illinois and Colorado. Not previously reported from our area, but taken by us in Medicine, Bear, and Shiningbank lakes all in the Athabasca River basin in the vicinity of Edson, Alberta.

Taxonomic Notes

The Iowa darter was first described as *Boleichthys exilis* from the upper Missouri River by Girard in 1859. It has been placed by some in the genus *Poecilichthys.* Synonyms include *Boleichthys warreni, B. fusiformis, Etheostoma iowae,* and *E. quappella.*

Development of scales on the cheek, nape, and breast, extent of the lateral line, and degree of fusion of the branchiostegal membranes all differ widely in populations from different places. Manitoba and Alberta specimens are divergent in these characters.

Postglacial Dispersal

The Iowa darter has moved north after glacial retreat, to occupy Hudson and James bay drainages as well as the Great Lakes system. The Alberta collections within our area lie north of the McLeod River, a tributary of the Athabasca, so the species may be established over a wider area within the upper Mackenzie River basin than present collections indicate. Western and eastern specimens differ in a manner suggesting that the species may have occupied more than one refuge south of the ice sheet. A distinctive stock in the upper Missouri (perhaps originating from the preglacial Hudson Bay drainage described under "Geological History") may have moved north and crossed into the arctic watershed in the extreme northwest of its range.

Biology

Unfortunately little is known of the biology of the species in the arctic watershed, where it has been discovered only recently. Collections in our area have been from the shallows of clear sand or mud-bottomed lakes. Elsewhere Iowa darters occur in lakes or rivers where the silted bottom has a small amount of aquatic vegetation, or occasionally in faster gravelly streams. Darters in our collections had fed on small clams, or amphipods, or aquatic insect larvae, and on large crustacean plankton.

Spawning is said to occur elsewhere at ages 1–3, in April and May; the eggs are laid in the slow current of streams that contain some vegetation and submerged fibrous root banks, or over similar bottoms of lake shores (Winn, 1958). A territory of 30–60 cm in diameter is defended against other fish. After courtship, the female rests on the bottom horizontally or tilted up at 45°. The male rests on top of her, the two vibrate rapidly; sperm and 3–7 eggs are released simultaneously. A female may thus spawn several times with one male; one female lays from about 550 to 2000 eggs in a season. The adhesive eggs, about 1.1 mm in diameter, hatch in about 18 days at 13 C (55.4 F) (Winn, 1958).

This fish has the smallest adult size of any species in our area. It is also our only representative of the darters, a diverse group of highly specialized little animals. Forbes and Richardson (1920) wrote enthusiastically of darters "Peculiar to this country, in which the subfamily has a great development, interesting in their variety, their habits, and their relations to nature, and especially attractive by reason of their graceful forms, their relatively minute size, their brilliant colouration, and the exquisite detail and finish of their structural equipment, they are to the fishes of North America what the humming-birds are to South American birds. They seem not to be so much dwarfed as concentrated fishes, each embodying in a small space all the complexity, spirit and activity of a perch or a wall-eyed pike."

THE FLOUNDERS — Family PLEURONECTIDAE

The flounders are flatfishes in which the eyes and coloured surface are on one side of the body (see sketch in Key to Families). In most flounders the eyes are on the right side, but in arctic waters the starry flounder (*Platichthys stellatus*) usually has its eyes on the left side. None of the flounders in our area is a strictly freshwater fish, but two species (*Liopsetta glacialis* and *Platichthys stellatus*) commonly enter the lower portions of rivers.

KEY TO THE SPECIES

1(2) Skin alongside the lateral line smooth; dorsal and anal fins clear or with diffuse dusky spots, without bars .... Arctic flounder, *Liopsetta glacialis* (Pallas)

A greyish or brownish flatfish with irregular speckles or blotches. Ranges in the arctic from the White Sea in Europe east at least to Bathurst Inlet, and south to the Sea of Okhotsk and the Alaska Peninsula.

2(1) Skin alongside the lateral line rough; dorsal and anal fins with distinct black and white bars .... Starry flounder, *Platichthys stellatus* (Pallas)

A distinctive coloured flatfish, frequently found in fresh water, but apparently not breeding there. Ranges in the arctic from Bathurst Inlet to Bering Strait, and south in the Pacific to California and to Korea.

COLLECTING AND PRESERVING SPECIMENS

COLLECTING AND PRESERVING SPECIMENS

This account is prepared for interested persons who may wish to preserve specimens for identification by specialists. It is not meant as a guide for collecting fishes on a professional scale. Those interested in making extensive collections should refer to Chapter VI of Bulletin 69, National Museums of Canada, Revised Edition, 1965, *Methods of Collecting and Preserving Vertebrate Animals.*

What To Collect

The area covered by this Bulletin has been so poorly collected that almost any fish taken in the area will be of some scientific value. Areas in which the fish fauna is virtually unknown are the northern Yukon Territory (north of Dawson City), the middle Mackenzie River system (from Fort Providence to Arctic Red River), and the entire districts of Keewatin and Franklin. Anyone who lives or works in these areas, and is interested in fishes, should not hesitate to send specimens for identification. Fishes that are of particular scientific interest are lampreys, whitefish (especially ciscoes), minnows (Cyprinidae), suckers, and sculpins.

How To Preserve Fish

The best preservative is 10% formalin, made by adding 1 part of concentrated formalin to 9 parts of water. Concentrated formalin can be purchased at drug stores and from supply shops. It is poisonous and the fumes are irritating. Care should be taken when using formalin to keep it away from cuts, and from the eyes. Specimens should be freshly killed when placed in 10% formalin. If the fish is over 8 inches long, a slit should be made in the right side to allow the preservative to penetrate into the body cavity. The body should be straight and not unduly crowded. The volume of preservative should equal the volume of specimens.

If formalin is not available, other preservatives can be used. Anything with a high alcohol content will do: whisky, rum, gin, rubbing alcohol, or alcohol-based shaving lotions. A strong brine solution (1 lb of salt in a gallon of water) is also effective for short-term preservation. Specimens may be frozen, and later thawed and preserved in formalin.

If because of space or hunger the whole fish cannot be preserved, the most valuable part to save for identification is the head, cut off so as to include the pectoral fins.

When preserving a fish, a label should be placed in the container along with the specimen. The label should be of stout paper (flimsy paper will come apart in preservative) and written in pencil. The only satisfactory ink is waterproof india ink.

The minimum information to include on a label is the date, locality, and collector's name. The locality is all-important and should be clearly designated. This is particularly true in the North where many waterbodies have local names that do not appear on maps. The best system is to indicate the watershed as well as the exact locality, and the distance from the nearest settlement (e.g., mouth of Wind River, Peel River system, 130 miles south of Fort McPherson, N.W.T.).

Shipping Specimens

Specimens should not be shipped until they have been in preservative at least 1 week. After a week in preservative the fluid may be drained off and the specimens and label wrapped in gauze and tied with string. If gauze is not available, any cloth will do. The wrapped specimens should then be placed in a plastic bag and finally in a sealed shipping container. Small cans, boxes, or mailing tubes make good shipping containers. Any empty space in the container should be stuffed with wood chips, moss, cloth, or paper. Frozen specimens can be shipped by air in plastic bags packed in styrofoam coolers or other insulating containers, provided arrangements have been made with the recipients in advance.

Where To Ship Specimens

A number of institutions have a scientific interest in northern fishes. They include:

Alaska — Dr J. E. Morrow
Department of Wildlife Management
University of Alaska
College, Alaska

Canada — Curator of Fishes
Institute of Animal Resource Ecology
The University of British Columbia
Vancouver 8, B.C.

Dr C. C. Lindsey
Department of Zoology
The University of Manitoba
Winnipeg 19, Man.

Curator of Fishes
Royal Ontario Museum
Toronto, Ont.

Curator of Fishes
National Museum of Natural Sciences
National Museums of Canada
Ottawa, Ont.

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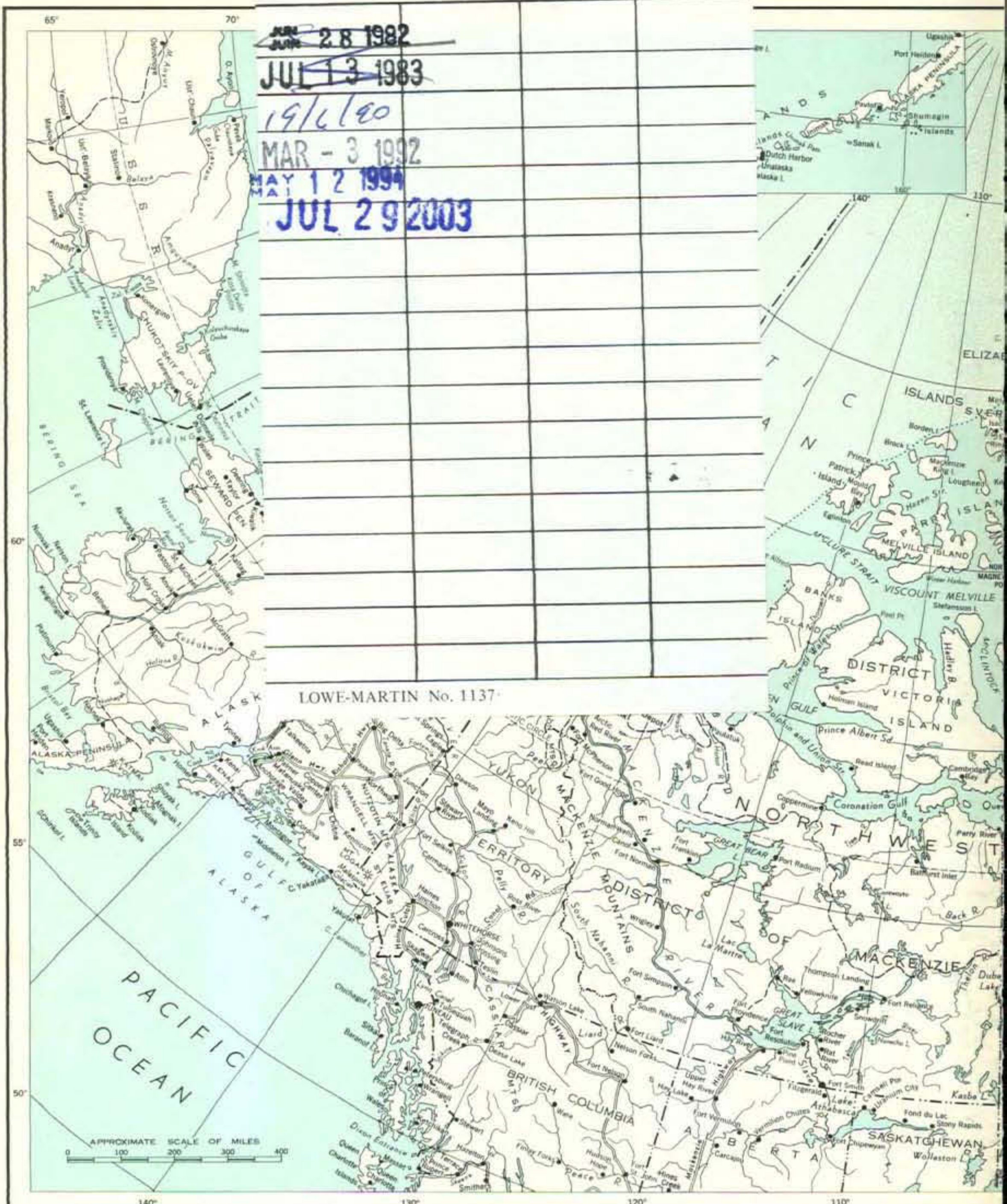

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SEWARD PEN.
YUKON TERRITORY
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DISTRICT OF MACKENZIE
NORTHWEST
DISTRICT
VICTORIA ISLAND
BANKS ISLAND
MELVILLE ISLAND
VISCOUNT MELVILLE
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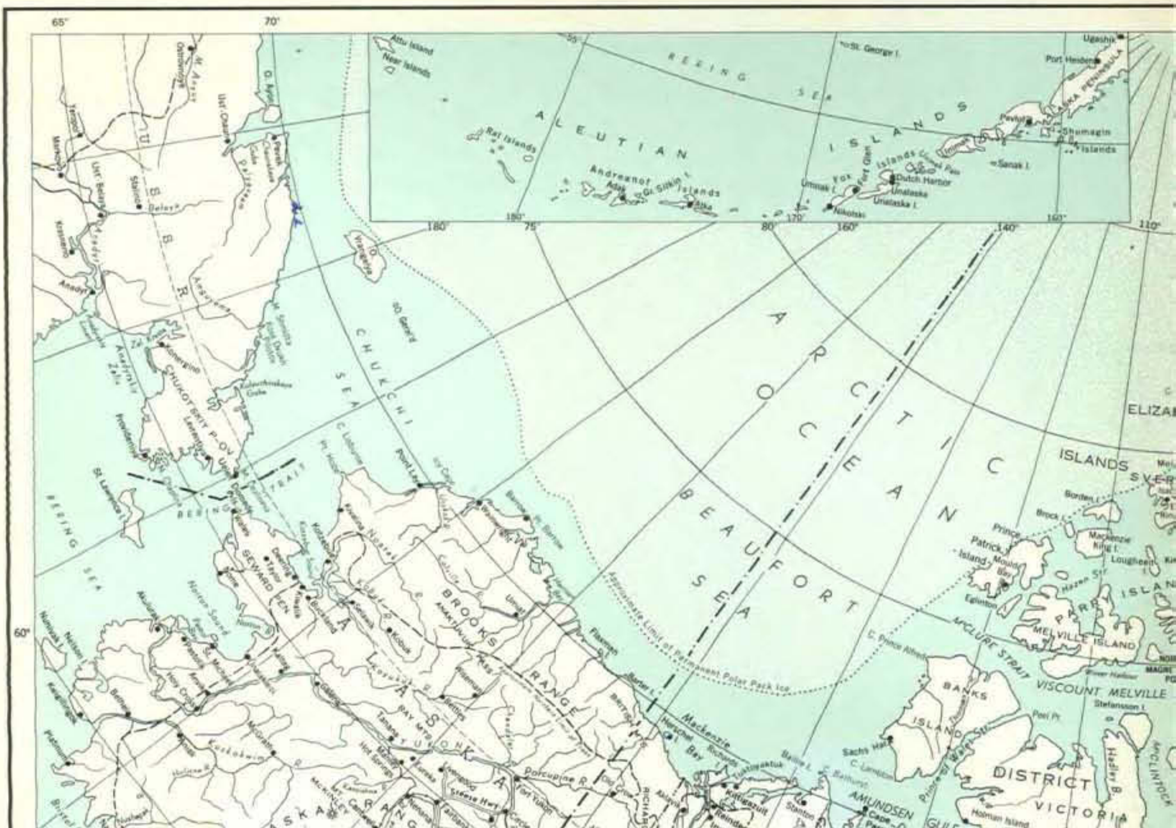
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GULF OF ALASKA
PACIFIC OCEAN
YUKON TERRITORY
WHITEHORSE
MACKENZIE MOUNTAINS
DISTRICT OF MACKENZIE
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GREAT SLAVE LAKE
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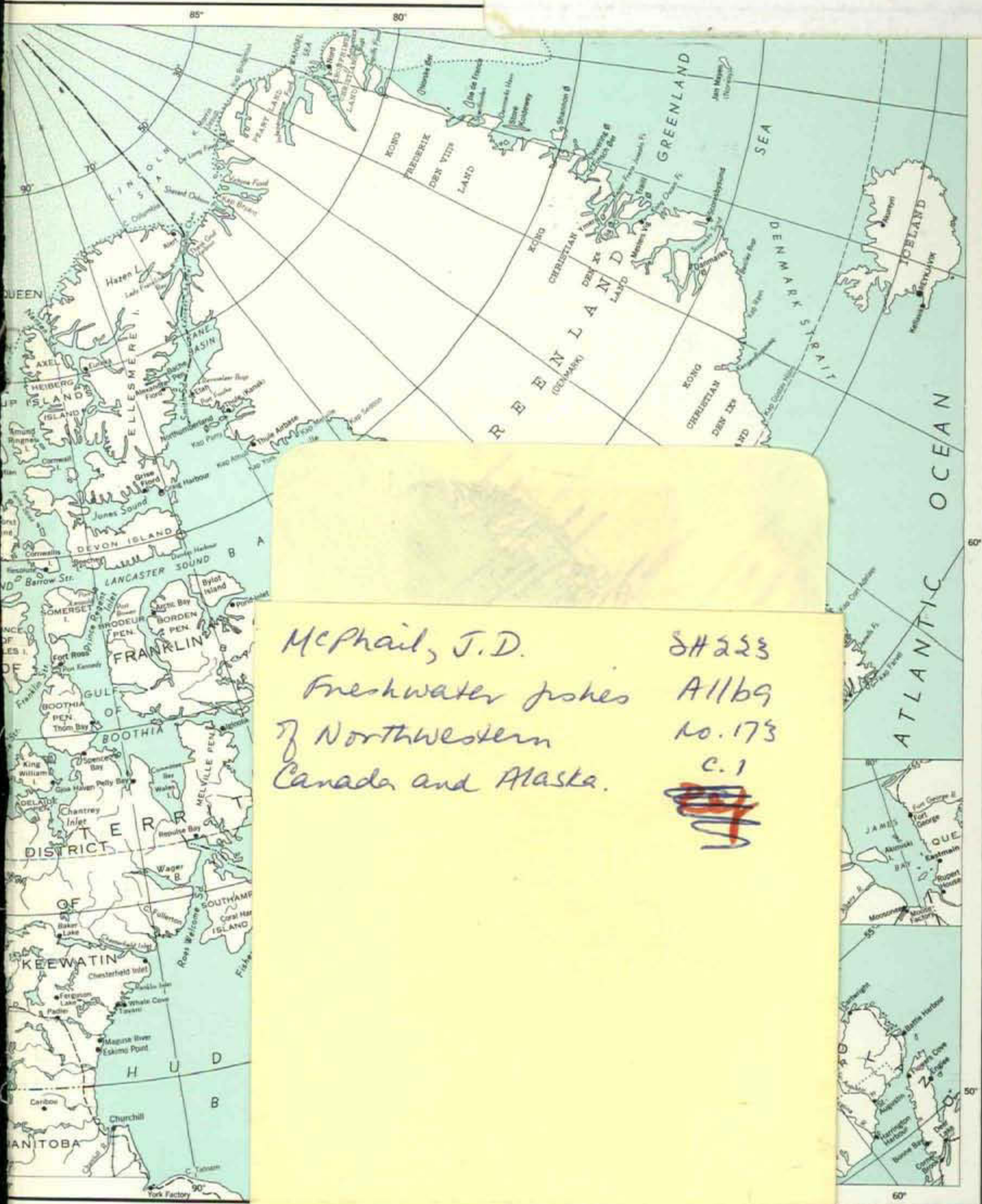
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DENMARK STRAIT
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ELLESMERE I.
DEVON ISLAND
LANCASTER SOUND
Jones Sound
FRANKLIN
GULF OF BOOTHIA
DISTRICT OF KEEWATIN
Churchill
MANITOBA
York Factory
JAMES BAY
NG BRANCH, OTTAWA, CANADA, 1964