BIOGEOGRAPHICAL AND ECOLOGICAL FACTORS CONTRIBUTING TO THE DECLINE OF ARCTIC GRAYLING, *THYMALLUS ARCTICUS* PALLAS, IN MICHIGAN AND MONTANA

by
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PREFACE

Often studies and discussions of extinction are permeated with emotion. Such overtones detract from a rational examination of the facts. All things considered, what constitutes extinction? Is it when a species ceases to exist? If so, the term does not apply to arctic grayling since, although it has disappeared in historic times from parts of its range, other populations of the same species still flourish in Siberia, Alaska, and Canada. Over the years the grayling of Michigan has been classified as a separate species, subspecies, and now race. Was it extinct when classified a species but not when classified a race? Can the term extinction be rightfully applied when a small peripheral population on the edge of a thriving population dies off? When is a specific population separate from the remainder of the species? Ultimately, extinction takes place whenever an individual organism dies. For this reason the term range adjustment is more widely applicable than extinction.

A historical study of the present type places heavy dependence upon early American literature pertaining to wildlife. The University of Michigan Libraries, Michigan Historical Collections, Montana Historical Museum, and Dr. Reeve M. Bailey's reprint collection have been a source of relevant material.

Interviews were made with 26 early settlers in Montana and 8 in Michigan. By 1895 grayling had disappeared from much of Michigan, so there are few people, having firsthand knowledge of the fish, old enough to remember that period. In many instances I have used ideas and information derived from interviews without giving individual credit. Often information was of little value until interpreted in light of what someone else had written or said, and at other times I took the liberty of qualifying, expanding, or restricting information according to the background of the source.

As much as possible, personal viewpoints of early writers have been avoided unless their ideas were based on sound observations. Many people have written their interpretation of why arctic grayling has declined, but this was almost always based upon a restricted point of view or upon prejudiced ideas. However, untrained observers must be given credit for usually recognizing grayling (although sometimes confused with whitefish), for knowing how many they caught, the date, and where the catch was made.

Because information had to be gathered from what some may consider sources of questionable accuracy (sporting magazines, recall of 95-year-old people, etc.), an attempt was made to avoid reaching a conclusion from just one or two sources. Also, if the information were incorrect by a few years, the results would not be materially different. The lack of sufficient data necessitated using certain watersheds or areas almost to the exclusion of others. Thus, much of the Michigan work must be based upon the Manistee and Au Sable rivers since they attracted most attention as grayling waters.

It was necessary to restrict the scope of the problem. Existing grayling taxonomy is accepted, although it is admittedly in need of comprehensive work. The cutthroat trout in Montana has undergone a decline much like that of grayling. Some hypothetical causes of drastic population reduction, such as epizootics, have not been discussed.

Stream names frequently lead to confusion. Such common names as Pine River or Clear Creek are found in almost every drainage. Even when the county was specified, the particular stream to which a writer referred was not always clear for more than one stream of that name may exist in a county. In such instances the information could not be used.

For brevity and clearness the following names are used in referring to the different grayling populations:

American grayling -- both the arctic and southern populations

Arctic grayling -- the arctic population in Canada and Alaska

Southern grayling -- the Montana and Michigan populations

Grayling -- the Montana or Michigan population

Montana grayling -- the grayling in Montana

Michigan grayling -- the grayling that was in Michigan

Probably all of the above should be called arctic grayling, but this would be unnecessarily cumbersome. Nomenclature, with the exceptions just listed, is from <u>A List of Common and Scientific Names of Fishes from the United States and Canada</u>, Second Edition, Special Publication No. 2, American Fisheries Society, 1960. The technical equivalents of the common names used in this paper may be found here.

I wish to express appreciation to Professor Stanley A. Cain

who directed my efforts and made this study possible. Professor Karl F. Lagler first planted the idea for the study and has continued to help in many ways. Other members of my doctoral committee helpfully criticized the manuscript. Many people have contributed information, suggestions, and cooperation; only a few can be named individually: Dr. Gerald P. Cooper, Michigan Institute for Fisheries Research; Dr. Reeve M. Bailey, University of Michigan Museums; Mr. T. B. Durling, Michigan Conservation Department; Mr. O. L. Wallis, National Park Service; Messrs. William Alvord, John J. Gaffney, and Nels A. Thorsen, Montana Fish and Game Department. My wife, Ruth Vincent, aided by typing and editing and by preparing the figures. Financial support was provided by the National Science Foundation. For twenty-one months I was employed as Research Associate on NSF grant No. G 14494 which was received by Professor Cain, my chairman.

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INTRODUCTION

The arctic grayling is a dramatic example of an animal that has made major range adjustments in comparatively recent times. Although the arctic grayling thrives within its main range to the north, one disjunct population (in Michigan) has become extinct and another (in Montana) has become greatly reduced in its range.

Clear cold-water salmonid fishes, graylings are found throughout the arctic and subarctic. They have stringent ecological requirements, are intolerant of pollution, and under certain conditions can attain very high population densities. Their striking appearance and large dorsal fin invite attention. Much has been written about American grayling, but no one has attempted a broad ecological analysis of forces operating to cause its decline.

Environmental change is continual and inevitable. Changes that occur faster than a species can genetically adapt to or migrate away from culminate in the extermination of peripheral populations. In this manner the focus of a species range moves with the environment. Generally, marginal populations are pinched off and lose genetic contact with the main population when change is rapid. Man's actions are often decisive in this regard, for he can alter an ecosystem beyond its limits of homeostasis or alter it faster than migration or adaptation can take place.

Since late Pleistocene, man has become an increasingly major influence upon the earth. His relationship to much of the biota has changed from commensalism to that of near-control. Nevertheless, man is a relatively new force on the earth. His rising technology and expanding skills easily give him the ability to modify existing conditions. Man, as the now dominant organism, can in many instances alter existing communities and environments in order to meet his own needs. Marsh (1874) was one of the first authors to point out man's activities in this regard. More recently a symposium published as Man's Role in Changing the Face of the Earth (Thomas, 1956) summarized much of the current thinking. Man has become such a widespread biological and geological force that Vernadsky (1945) inaugurated the term "noosphere" to add to the previous term "biosphere." This new word encompasses the concept of social and intellectual man in contrast to biological man.

Because of greater demands and increased capabilities, man is carrying on large-scale land- and water-use programs. Irrigation, drainage, flood control, forestry, cultivation, erosion prevention, dam construction, or urban expansion are developed according to man's desires. The effects—biological, economic, or physical—of these land-use programs reach beyond the immediate time and area. Frequently, non-anticipated secondary or tertiary conditions develop. When pressures for social and economic developments are great, the physical and subsequently the biological realms may be drastically modified.

Just what is the role of man's earth modification in range adjustment and extinction of other animals? Habitats are greatly altered, upsetting the natural balance of the community; formation of new genotypes by domestication is common; desirable forms are encouraged;

and undesirable forms, exterminated. This study concerns the role of habitat change in range adjustment and is an analysis of the factors of a species decline from a segment of its former range.

The grayling was chosen as subject of this study not because of the fish per se but because (1) there is considerable published material available, (2) the decline was recent enough that early settlers could provide information, (3) the two disjunct populations and the main northern population form a continuum that ranges from disappearing through declining to thriving conditions, (4) grayling populations appear to have been subjected to both climatic change and human changes so interaction can be studied, and (5) it can be presumed that southern populations are in tenuous balance with the environment, therefore being sensitive indicators of change.

Investigation proceeds from the hypothesis that the two disjunct, relict arctic grayling populations were near their limits of ecological tolerance because of climatic change and that conditions became progressively unfavorable because of three actions by white man: (1) land-use changes associated with agriculture and lumbering; (2) competition with exotic fishes, (3) over-exploitation of populations. Principal cause seems to be land-use changes and the implications that they have for grayling habitat. As each of these activities by white man were associated with land settlement and human population growth, they tended to interact during the same period.

Of necessity, this study is largely an historical one to which ecological reasoning can be applied, not an analysis of physical factors as such. As most population extinctions are not reported until afterward, little quantitative data exist. Thus, this is essentially an analysis by ecological reasoning through the employment of circumstantial evidence of phenomenom--decline and extinction--that cannot be approached directly. The conclusions should be evaluated in light of the nature of the problem and of the data. Although decline and extinction may be separated by definition, actually, one grades into the other.

The objectives of the study presented in this paper, therefore, are to appraise (1) the zoogeographical position of the grayling in relation to postglacial conditions, (2) the importance of over-exploitation by the fishery, (3) the effect of competition with exotic fishes, and (4) the role of land-use changes and subsequent aquatic habitat changes.

ZOOGEOGRAPHY

During glacial ages arctic and subarctic plants and animals moved alternately southward and northward with the advance or retreat of the ice front. Numerous northern species left small isolated populations in favorable habitats far to the south of their present main range. Many high-altitude and alpine biotas are partly a consequence of such disjunction as plants and animals remained after moving to these more nearly subarctic-like locations. Freshwater organisms had perhaps the most widely scattered and favorable refuges in the form of cold springs, deep lakes, subterranean and groundwater-fed streams—environments that are slower in adjusting to climatic changes. For this reason many of our well-known biotic relicts of glacial times are aquatic animals.

North Temperate freshwater fishes were also greatly affected by formation of temporary ice-dammed lakes, changed drainage patterns, different precipitation rates, and silt load of glacial-fed rivers. Periglacial lakes may have permitted movement to nearly all drainages; they may have existed for too short a period to be avenues of fish movement; or during their existence they may have been unsuitable habitat. Species with a narrow ecological tolerance must use geologically available routes at just the proper time before either the environment becomes unsuitable or the migration route closes. Glacial disturbance of the population plays a major role in genetic change.

Hybrid swarms are common because of several periods of range truncation and subsequent separating and joining of populations. Allopatric populations, which at one time shared the same gene pool, are isolated from one another. Adequate classification of these groups is difficult.

In this study it is basic to establish the distribution of grayling and its relationship to other community members, to climate, and to the biotic province.

Classification

The arctic grayling of North America, *Thymallus arcticus*, is a member of the holarctic (essentially arctic and subarctic) family, Salmonidae. The genus, *Thymallus*, includes four species: one is European, two are Asiatic, and one is both Asiatic and North American. These species form many local subspecies and races.

The relative taxonomic positions of the Montana and Michigan grayling are uncertain. Dr. Bean (Henshall, 1902; Henshall, 1906; and Jordan, 1905 and 1925) maintained the two as distinct species. However, Jordan (1891) previously questioned whether or not there was more than a slight difference between them. It seems that the Montana and Michigan grayling have differentiated an equal amount from the northern form (Henshall, 1898a). Later authorities generally considered the two southern populations as subspecies until Walters' work in 1955, after which they were grouped into the same subspecies. This then placed the northern American grayling as *Thymallus arcticus signifer* (Richardson) and the southern American grayling, from Michigan and Montana, as *Thymallus arcticus tricolor* Cope. Jordan (1905) and several other workers since have questioned the consistency of characters that separate the southern from the northern stocks. Lindsey (1957) noted that the relationship between these two is undetermined; Hubbs and Lagler (1958) also considered the southern forms inseparable from the northern form. Whether or not the separation of the northern and southern geographic stocks of American grayling into subspecies is warranted or whether the Michigan and Montana stocks should be separated at this level is uncertain (Norden, 1961).

Subspecific classification of grayling in America is in need of definitive study. Following is the classification of graylings and a listing of forms as they are now generally recognized (modified from Nikolskii, 1957; Norden, 1961; Svetovidov, 1936; and Walters, 1955):

- Clupeiformes
  - Salmonoidei
    - Salmonidae
      - *Thymallus* Cuvier, 1829
      - *T. thymallus thymallus* (Linnaeus), 1758, Europe
      - *T. arcticus arcticus* (Pallas), 1776, Western Siberia
      - *T. a. signifer* (Richardson), 1823, Eastern Siberia, Alaska, Canada
      - *T. a. tricolor* Cope, 1865, Montana, Michigan
      - *T. a. grubei* Dybowski, 1869, Amur River
      - *T. a. baicalensis* Dybowski, 1874, Lake Baikal
      - *T. brevirostris* Kessler, 1879, Northwestern Mongolia
      - *T. nigrescens* Dorogostajskij, 1923, Lake Kosogal, Mongolia

Distribution

The genus Thymallus is nearly circumpolar: a gap in distribution occurs from Hudson Bay eastward across Quebec, Newfoundland, Greenland, and coastal Norway. One species, arctic grayling, ranges from the Ural Mountains eastward across Siberia, Alaska, and Canada to Hudson Bay. Southward in Asia it is found to the headwaters of the Ob, Yenisei, Lena, and Amur rivers (Svetovidov, 1936). The range of arctic grayling continues in Alaska and Canada to the headwaters of the Bering Sea, Arctic Sea, and Hudson Bay drainages southward to, but not including, the Nelson River, Manitoba. In Pacific drainages arctic grayling is found in headwaters of the Susitna, Copper (Wojcik, 1955), Alsek, Taku, and Stikine rivers (Lindsey, 1956). Movement across the divide into these rivers was probably by headwater stream capture (Walters, 1955).

Distribution of arctic grayling is general across Alaska and Canada wherever habitat is suitable (Figure 1). Because of specific habitat requirements, however, distribution tends to be irregular within the range. No records could be found for northeastern Keewatin and the Melville Peninsula. Adequate collections may be wanting; suitable habitat may be absent; or the time limitation has not permitted grayling to occupy this area.

The southern limit is defined by waters of the Peace, Athabaska, and Churchill rivers. Introductions have extended the distribution into the North Saskatchewan River drainage (Lindsey, 1956). Along the west shore of Hudson Bay, arctic grayling is found in the Broad, Owl, and Silcox rivers south of the Churchill River (Dymond, 1947). None

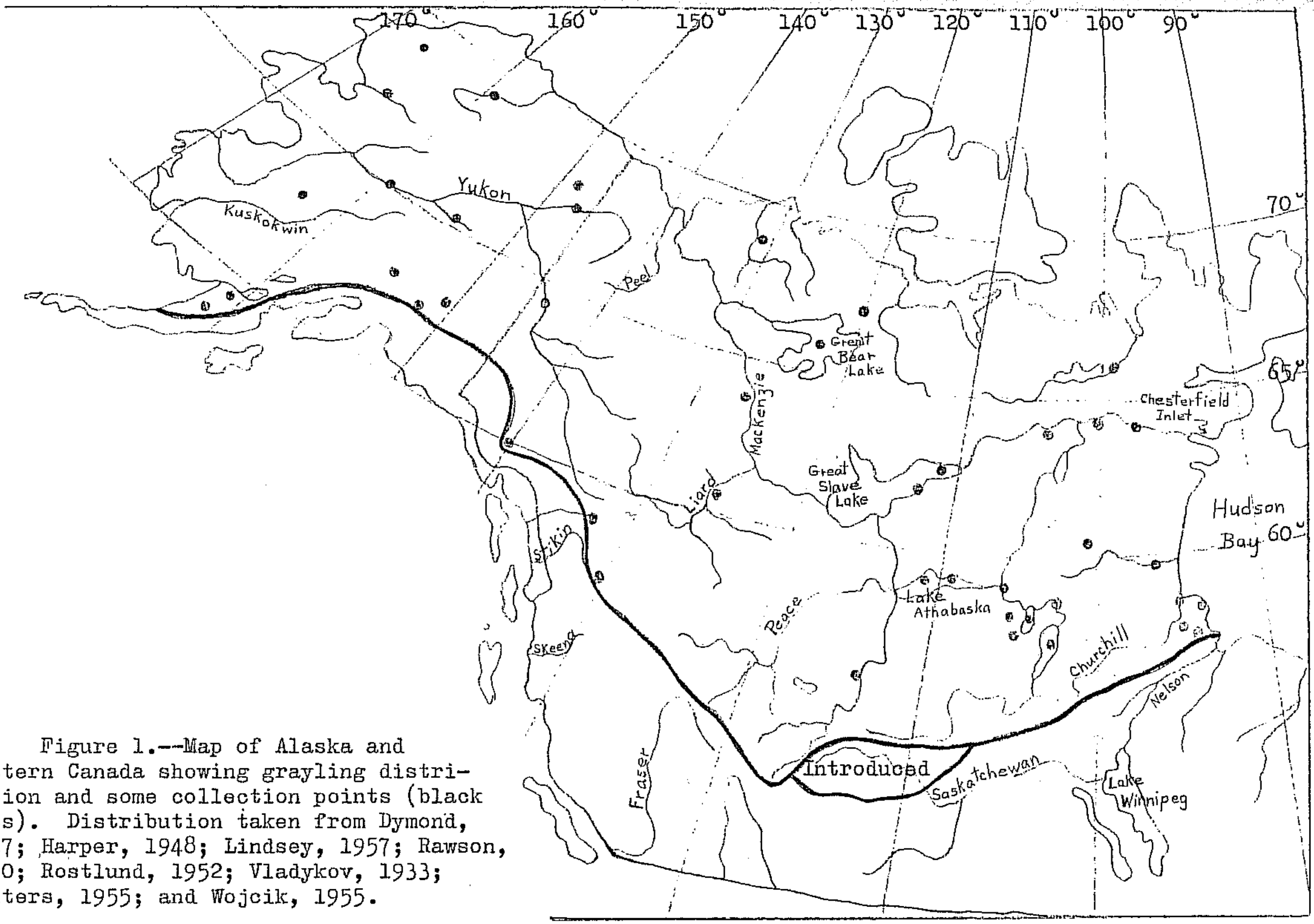

Figure 1.--Map of Alaska and Western Canada showing grayling distribution and some collection points (black dots). Distribution taken from Dymond, 1947; Harper, 1948; Lindsey, 1957; Rawson, 1950; Rostlund, 1952; Vladykov, 1933; Walters, 1955; and Wojcik, 1955.

was observed in the Nelson River only a few miles further south (Doan, 1948).

In Montana, the grayling is found generally upstream from Great Falls (Figure 2). According to limited available information, distribution has always been irregular. The Sun and Smith rivers were the only tributaries that had grayling below Three Forks. Reports of grayling in the Missouri River have come only from the vicinity of Craig. Evermann (1893) found none in tributaries below Three Forks or in the Blacktail, Ruby, or Boulder rivers of the Beaverhead-Jefferson drainage. Many of these tributaries and probably sections of the Missouri River lacked proper habitat. A steep gradient without flat mountain valleys is the most obvious difference.

The Montana grayling is not indigenous above barriers, whereas other species, especially cutthroat trout, are (Hanzel, 1959). The upper Sun and Dearborn rivers were probably devoid of all fish life until recent introductions. In the Madison River drainage, a single species, slimy sculpin, was native to the Gibbon River above a barrier, and the upper Firehole River had no fishes (Jordan, 1891).

The Michigan grayling apparently occupied all large streams in central Michigan north of the White River on the Lake Michigan side and of the Rifle River on the Lake Huron side (Figure 3). It was found only in the headwaters of the Rifle River, but none was ever reported from the nearby Tittabawassee River drainage. It occurred in a few western tributaries of the upper Muskegon River, mainly Hersey Creek. From the latter came the first reports of the species in Michigan in the early 1850's (Metcalf, 1961).

The Michigan grayling was mainly a stream-dwelling fish; reports

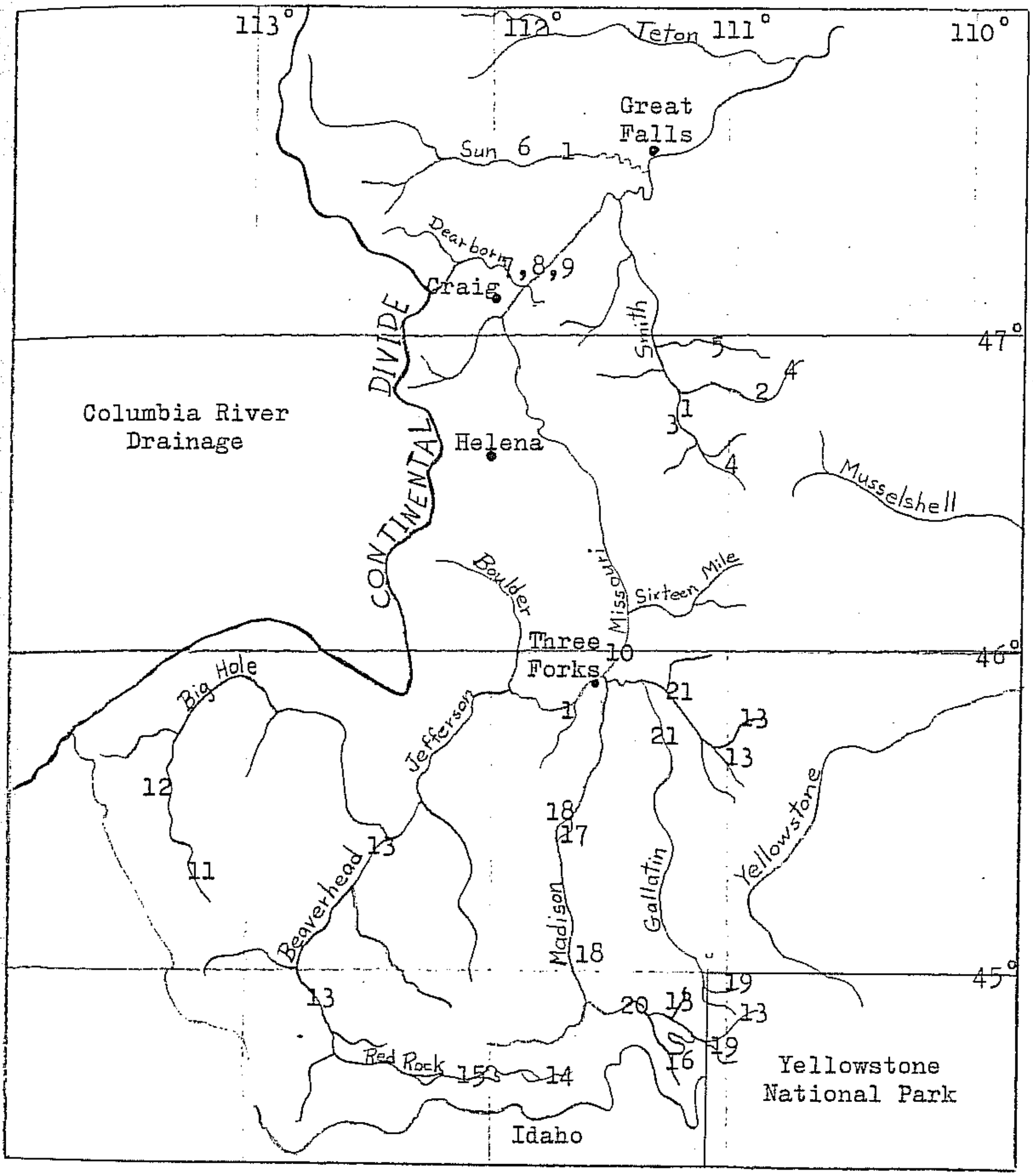

Figure 2.--Distribution of indigenous grayling in Montana. Records from: (1) Milner, 1873; (2) Head, 1874; (3) Ludlow, 1876; (4) Prisson, 1898; (5) Henshall, 1919; (6) Ford, interview (grayling present before 1900); (7) Hilger, 1929; (8) Eigenmann, 1894; (9) Ford, interview (grayling present in 1910); (10) Harris, 1887; (11) Boule, 1896; (12) Dunham, 1897; (13) Evermann, 1893; (14) Henshall, 1907; (15) Bean, interview (grayling present before 1900); (16) Dwelly, 1892; (17) Henshall, letter at Bozeman Fish Cultural Station, Nov., 1897; (18) Many early settlers, interviews (grayling present before 1900); (19) Jordan, 1891; (20) Kendall, 1915; (21) Many early settlers, interviews (grayling present before 1900).

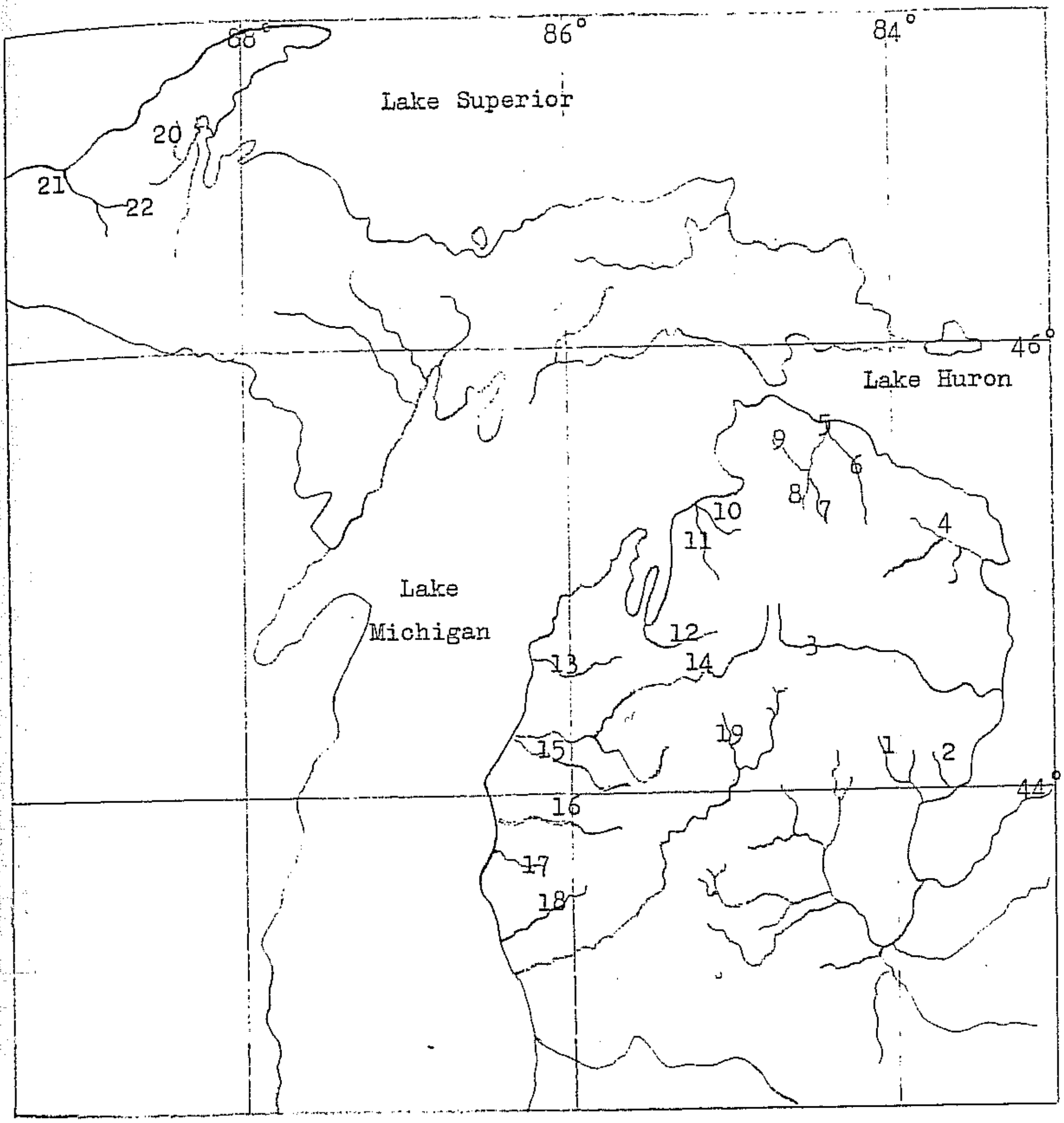

Figure 3.--Distribution of indigenous grayling in Michigan. Records are from: (1) Rifle--Bissell, 1890; Hallock, 1873a; Norris, 1879. (2) Au Gres--Milner, 1873. (3) Au Sable--See text. (4) Thunder Bay--Mather, 1874. (5) Cheboygan--Anonymous, 1874; Green, 1874; Northrup, 1880. (6) Black--Harris, 1905; Hough, 1902; Mershon, 1923. (7) Pigeon--Bissell, 1890; Henshall, 1919; Northrup, 1880. (8) Sturgeon --Beebe, 1879; Bissell, 1890; Norman, 1887. (9) Maple--Harris, 1905; Hough, 1899; Whitaker, 1887. (10) Boyne--See text. (11) Jordan--See text. (12) Boardman--See text. (13) Betsie--Bower, 1884. (14) Manistee--See text. (15) Little Manistee--Hallock, 1888; Macfie, 1895; Mershon, 1923. (16) Pere Marquette--Mershon, 1923; Milner, 1873; Whitaker, 1887. (17) Pentwater--E. D. R., 1885. (18) White--Bissell, 1890. (19) Hersey--Metcalf, 1961; Milner, 1873; Rough, 1887. (20) Otter --Taylor, 1954. (21) Little Carp Lake--Ruthven, 1906. (22) East Branch Ontonagon--Bissell, 1890.

of lake-dwelling populations are rare. One of these was from some north-central lakes (Hallock, 1877) of the Lower Peninsula, and another was from Fife Lake of the Manistee River drainage (Harris, 1884). Henshall (1919) even reported catching grayling while fishing for ciscoes in Lake Michigan at Charlevoix. The species was also taken from the lower reaches of the Manistee, Cheboygan, and Au Sable rivers (Green, 1874; Norris, 1879).

The Otter River, in the Sturgeon River drainage, is the only river in the Upper Peninsula of Michigan from which reliable records of the grayling exist. Following its discovery there in 1885, the fish never occupied more than a 6 to 10-mile stretch of the river (East, 1930). Ruthven (1906) saw some specimens which were said to have come from Little Carp Lake, Ontonagon County, and Bissell (1890) said that the East Branch of the Ontonagon River, but possibly meant the Otter River, had them too. The validity of these single observations may rightfully be questioned. One short section of the Otter River is the only stream in the Great Lakes drainage outside of the Lower Peninsula from which grayling has ever been authentically reported. Several other species with localized distribution in the Great Lakes are found in this river system: lake sturgeon, bigmouth shiner, silver redhorse, and sauger.

Broken distribution between Western and Central United States is not unique. The Keweenaw Peninsula of Upper Michigan possesses a well-marked element of isolated Rocky Mountain and Pacific Coast plants (Fernald, 1925). The pigmy whitefish is found in isolated places along the Pacific slope, including only two Western Montana lakes (Weisel, 1957), and in the depths of Lake Superior. Two closely related genera of mudminnows are found, separated, in Washington State and Central United States, respectively.

The distribution of American grayling, therefore, is widespread and continual across Alaska and northern Canada, plus two disjunct populations that are or were approximately 500 (Montana) and 800 (Michigan) miles south of the main range. Furthermore, the Otter River population was approximately 175 miles from the remainder of the Michigan population.

The two disjunct populations lie on the southern border of a boundary line for the distribution of many other fishes. Numerous fishes have a range that extends northward to central Michigan or westward to Great Falls, Montana. Examples of species whose distribution stops at central Michigan are spotted gar, northern hog sucker, lake chubsucker, spotted sucker, river redhorse, warmouth, and white crappie. Species that are found westward up the Missouri River to the vicinity of Great Falls include shovelnose sturgeon, goldeneye, river carpsucker, northern redhorse, and channel catfish. Other species associated with grayling do not range much further south than these areas as, for example, several species of whitefishes, lake trout, northern pike, longnose sucker, and burbot. In Michigan the southern limit of distribution coincided with that of the Hemlock-Hardwood Forest vegetation type, and in Montana the downstream or eastward limit approximates that of the Boreal Forest vegetation type (Oosting, 1958). Following the biome concept, many birds, mammals, and other animals have a distributional restriction at this boundary. The two disjunct grayling populations are located along the southern fringe of their respective biotic provinces or more broadly at the edge of the taiga biome (Allee *et al*., 1949).

The more-recent distribution of self-sustaining southern grayling populations is approximately as follows:

Montana	21 lakes and 29 streams	Nelson, 1954
Montana, Glacier National Park	1 lake	Pers. comm., W. M. Morton
Wyoming	4 or 5 lakes	Simon, 1951
Utah	20 lakes	Dotson, 1961
Colorado	3 lakes	Pers. comm., W. R. Seaman
Washington	2 lakes	Pers. comm., Cliff Millenbach

Nearly all stem from introductions. Some are not thriving populations, especially those listed in Montana. All populations outside of Montana are in high-altitude lakes where they receive little fishing pressure and where limited grazing is the major land use.

Climatic change and temperature

The climate has become warmer since the last continental glaciation, with many fluctuations as shown by Dorf (1960) in his review of past and recent climatic changes. Mid-latitude postglacial air temperatures have risen a magnitude of 5 to 8° F. (Flint, 1957).

It is evident that North Temperate plants and animals have been shifting northward following deglaciation. (See Just, 1959, for a review of vegetation and Flint, 1957, for a review of animals.) Distribution of the grayling has been adjusting just as other species to the slow climatic warming. Possibly only through ground water and meltwater streams has suitable habitat been maintained as far south as the historic range of the species.

Air and water temperatures have a complex relationship. Runoff-fed streams typically have wide seasonal temperature fluctuations corresponding with air temperatures. Macan (1958) concluded that small streams do not flow far before reaching a temperature equilibrium with the air. Lake surface water temperatures have a subdued response to air temperatures (McCombie, 1959). Ground water temperature at 30 to 60 feet is 2 to 3° F. above mean annual air temperature (Todd, 1959). Therefore, grayling, which commonly inhabits meltwater- and spring-fed streams, occupies an environment that responds slowly to increased air temperatures.

Present southern range of grayling across Canada more or less follows the 60° F. summer isotherm, but distribution in Michigan (southward) and in Montana (downstream or northeastward) closely approximates the 65° F. summer isotherm. However, cool water temperatures, because of water source, may compensate for high air temperatures. As discussed previously, southward distribution in Canada may not be limited by temperature but by other factors. Nevertheless, the example illustrates that in some areas cool water temperatures can counterbalance high air temperatures.

Temperature as an ecological barrier to fish distribution is common. For example, Radforth (1944) noted the significance of the 65 and 70° F. July isotherms in the northward distribution of Ontario fishes. Furthermore, Séquin (1956) showed that southward distribution of brook trout in the Appalachian Mountains is limited by the 70° F. summer isotherm. Since a major ecological demarcation and topographic change occurs along the border of grayling distribution in both Michigan and Montana, it is doubtful if a simple temperature relationship has restricted the spread of southern grayling populations.

Given sufficient time, water temperatures even in these favorable sites would have become critical. There are indications, however, that competition from recent invading fishes and man-caused habitat changes became limiting before water temperatures. The nearness of a climatic threshold is suggested by the droughts of 1890 and 1930 in Montana that caused direct grayling mortality and adversely changed the habitat. Under optimum environments, low-water conditions may not have been critical.

It is nearly impossible to determine if present stream temperatures within present or past grayling range are near a critical level. Maximum water temperatures that grayling can withstand are unknown and grayling in some rivers move away from adverse water conditions for part of the year. High water temperatures may not be as critical as absence of a cool-water tributary or spring hole into which grayling may move for short periods. In the ex-grayling streams of Michigan, water temperatures reach a maximum in the low seventies (water-temperature records, U.S. Geol. Surv., Lansing, Michigan). There is no way to compare these temperatures with those when grayling was abundant. Nor can comparison be made with grayling habitat in Western United States where all thriving populations are in lakes. In nearly every instance natural geologic warming of grayling streams has been accelerated by human activities such as removal of stream-side vegetation, reservoirs, return of irrigation water, or other human activities that reduce stream flows.

The Grayling Community and Origin of Its Members

In its typical stream or littoral community, the grayling is associated with few other fishes. The grayling community of the upper Missouri River includes eight members; Big Delta Clearwater River, Alaska, five members; and Great Slave Lake, six members. Suckers, a shiner, pike, and whitefish are the only other fishes mentioned by early observers as associated with grayling in Michigan streams (Hallock, 1873b; Mather, 1874 and 1875; Oatka, 1888). The depauperate fish fauna characteristic of the arctic and subarctic is further reduced by the specific habitat of grayling. The Otter River, Michigan, is an exception, for this grayling community included approximately 20 species (Taylor, 1954).

In contrast to the small number of associate fishes in any one community, the grayling inhabits waters that contain a wide variety of fishes in different areas of North America (Table 1). The Tanana River, Alaska, has a strong Bering Sea drainage element; the upper Peace River, a western element; the upper Missouri River, a weak western element; and the Otter River, a strong eastern element. Only two species are found with grayling in all of the communities. These two, plus another four or five species that are found in five of the six communities, are forms that do well in both lakes and streams. Species most frequently associated with grayling tend to be lowland species--northern pike, suckers, and burbot--or deep lake species--lake trout, whitefishes, and lake chub. Although the southern grayling was essentially a stream inhabitant, the arctic grayling is also found in lakes. The European and Siberian graylings are rarely found in lakes except for the Lake Baikal form which also spawns on the lake

TABLE 1.--Distribution and probable Pleistocene refuges of fishes associated with grayling at six sites within its range. Distribution records are from: Wojcik (1955), Tanana River, Alaska; Miller (1947), Great Bear Lake; Lindsey (1957), Upper Peace River; Rawson (1959), Wollaston Lake, Saskat.; various sources, Upper Missouri River; Taylor (1954), Otter River. Refuges are designated by B for the Bering slope, Alaska, M for Mississippi or Atlantic drainages, and W for Pacific drainages.

Common names	Probable refuge	Tanana River	Great Bear Lake	Upper Peace River	Wollaston Lake	Upper Missouri River	Otter River
Silver salmon	B	X	–	–	–	–	–
Sockeye salmon	B	X	–	–	–	–	–
Chinook salmon	B	X	–	–	–	–	–
Inconnu	B	X	–	–	–	–	–
Lamprey	B	X	–	–	–	–	–
Arctic grayling	BM	X	X	X	X	X	X
Longnose sucker	BM	X	X	X	X	X	X
Burbot	BM	X	X	X	X	X	X
Northern pike	BM	X	X	X	X	–	–
Round whitefish	BM	X	X	–	X	–	–
Slimy sculpin	BM	X	–	X	X	–	X
Lake chub	M	X	–	X	X	X	X
Lake trout	BM	–	X	X	X	X	–
Lake whitefish	BM	–	X	X	X	–	–
Trout-perch	M	–	X	X	X	–	–
Walleye	M	–	X	X	–	–	–
Cisco	M?	–	X	–	X	–	–
Ninespine stickleback	B	–	X	–	X	–	–
Flathead chub	W	–	–	X	–	X	–

TABLE 1.--Continued.

Common names	Probable refuge	Tanana River	Great Bear Lake	Upper Peace River	Wollaston Lake	Upper Missouri River	Otter River
Dolly Varden	W	–	–	X	–	–	–
Brassy minnow	M	–	–	X	–	–	–
Northern squawfish	W	–	–	X	–	–	–
Largescale sucker	W	–	–	X	–	–	–
Peamouth	W	–	–	X	–	–	–
Redside shiner	W	–	–	X	–	–	–
Prickly sculpin	W	–	–	X	–	–	–
Pearl dace	M	–	–	X	–	–	–
Northern redbelly dace	M	–	–	X	–	–	X
Brook stickleback	M	–	–	X	–	–	X
Spoonhead sculpin	M	–	–	X	X	–	–
Mountain whitefish	W	–	–	X	–	X	–
Longnose dace	M	–	–	X	–	X	X
White sucker	M	–	–	X	X	X	X
Yellow perch	M	–	–	–	X	–	–
Spottail shiner	M	–	–	–	X	–	–
Emerald shiner	M	–	–	–	X	–	–
Fourhorn sculpin	M	–	–	–	X	–	–
Mottled sculpin	M	–	–	–	–	X	X

TABLE 1.--Continued.

Common names	Probable refuge	Tanana River	Great Bear Lake	Upper Peace River	Wollaston Lake	Upper Missouri River	Otter River
Mountain sucker	W	-	-	-	-	X	-
Cutthroat trout	W	-	-	-	-	X	-
Stone cat	M	-	-	-	-	X	-
Lamprey	M	-	-	-	-	-	X
Creek chub	M	-	-	-	-	-	X
Blacknose dace	M	-	-	-	-	-	X
Logperch	M	-	-	-	-	-	X
Johnny darter	M	-	-	-	-	-	X
Bigmouth shiner	M	-	-	-	-	-	X
Finescale dace	M	-	-	-	-	-	X
Bluntnose minnow	M	-	-	-	-	-	X
Flathead minnow	M	-	-	-	-	-	X
Brook trout	M	-	-	-	-	-	X

shoals (Nikolskii, 1957). Prof. H. Watling at Montana State University in an anatomical study of grayling nares found them of the type associated with lake-inhabiting species (pers. comm.).

The wide variety of fishes with which it associates and the generally few species found in any one community suggest that grayling is distributed over a wide ecological area. Three communities have a different trout that could compete with grayling: Dolly Varden trout in the Peace River, cutthroat trout in the upper Missouri, and brook trout in the Otter River. Young Pacific salmons probably occupy this same niche in the Tanana River. Throughout most of its northern range the arctic char complex occupies lower stream reaches near the coast and grayling, the middle and upper.

None of the species known to have been only in Alaska during glaciation is widespread in interior North America (Table 2).

TABLE 2.—A summary of the number of species utilizing Pleistocene refuges.

Location of fish community	Refuge area			
	Bering slope	Mississippi-Atlantic	Bering and Mississippi	Pacific slope
Tanana River	5	1	6	0
Great Bear Lake	0	3	8	0
Upper Peace River	0	10	7	8
Wollaston Lake	0	9	9	0
Upper Missouri River	0	4	4	3
Otter River	0	16	4	0

Conversely, only one species from the Mississippi drainage has reached the Tanana River. It therefore seems likely that widespread species had at least two refuges. From this evidence alone it is probable that grayling lived both northwest and south of the last ice sheet.

Discussion

There were four refuge areas where fishes could have survived the last glaciation: the Bering Sea drainage, the Pacific slope and Great Basin south of the ice front, the vast Mississippi River drainage, and the Atlantic slope. The grayling has never been reported in either the Pacific or Atlantic drainages so these areas were undoubtedly not used. The Bering slope, on the other hand, was certainly a refuge.

Widespread distribution in Alaska indicates access for a long period; similarity with eastern Siberian grayling (same subspecies, Walters, 1955) suggests recent genetic exchange across the Bering land bridge; Lindsey (pers. comm.) found the essentially freshwater fishes, arctic grayling, slimy sculpin, and Alaska blackfish, on St. Lawrence Island in the Bering Sea. It seems that these, as well as other arctic fishes (Walters, 1955), had ready access across the Bering land connection. With rising sea waters the three freshwater species found refuge on St. Lawrence Island from the marine environment.

As the Cordilleran and later the Keewatin ice sheet melted, the arctic grayling from the Yukon River drainage could move south and east. Probably the present Canadian grayling population came from this source. Headwater access from the Yukon River to the Mackenzie River drainage is comparatively easy. The Mackenzie River system then connects all the way to the Churchill River at the southeastern extremity of arctic grayling distribution in Canada. The arctic grayling, along with round whitefish and northern pike in some waters, has invaded the headwaters of five major Pacific coastal rivers south to the Stikine River. At the Skeena and Fraser-Peace rivers divide, several species normally associated with arctic grayling have crossed from east to west (Lindsey, 1956), but not arctic grayling. Considering its ready movement over divides to the north, comparatively recent arrival at this section of its range may not have permitted time for transfer by headwater stream capture. Recent successful introductions of arctic grayling into the North Saskatchewan River drainage suggest that an ecological barrier has not prevented further southward expansion.

Assuming that the northern population advanced southward, the two southern populations did not originate post-glacially from the northern population. Walters (1955) pointed out that lake trout must not have been in Alaska during glaciation as it is the only arctic Alaskan freshwater fish that is not also found in Siberia. An additional factor is the possible influence of parasitic lampreys. The lake trout is absent from lower reaches of all Pacific Coast or Bering Sea drainages that have parasitic lampreys.

Several species have a distributional skip that suggest two centers of postglacial redispersal. The slimy sculpin is found from the Great Lakes drainage north and westward through northern Canada and Alaska but is absent from most of the Saskatchewan River (Lindsey, 1956). A relict population of slimy sculpin in northeastern Iowa (Hubbs and Lagler, 1958) and its presence on St. Lawrence Island indicate two centers of dispersion (see McAllister and Lindsey, 1960). The round whitefish has an extensive distributional gap. Widespread across arctic Asia and America and abundant in the upper Great Lakes and glacial lakes of New York and the New England States, the round whitefish is absent from western and northern Ontario (Radforth, 1944) and all except the very northern parts of Manitoba, Saskatchewan, and Alberta (Hinks, 1943; Rawson, 1947a). Inasmuch as it is found both in Siberia and in glacial lakes of northeastern United States, two Pleistocene refuges are suggested from which round whitefish dispersed postglacially.

There are different opinions regarding the possibility of suitable habitat for clearwater fishes south of the ice front. Hubbs and Lagler (1958) and Radforth (1944) felt that most of the clearwater species moved southeastward from Alaska, whereas Walters (1955) and Wynne-Edwards (1947a) believed that both Mississippi and Bering refuges were used by salmonid fishes.

Certainly, environmental conditions could hardly be optimum for clearwater species below the ice front. Species, such as the lake trout, that inhabit large deep lakes or lowland species as the white sucker would find a more suitable environment than grayling that requires clear upland streams or shallow clearwater lakes. Today in Alaska and Canada arctic grayling has an irregular distribution in clearwater streams and avoids silt-ladened ones. That grayling is not found in Ontario, headwaters of the Missouri River tributaries as the Yellowstone, Judith, and Musselshell rivers, and headwaters of the Saskatchewan River indicates it did not thrive and become widespread in periglacial environments.

Three species, brook trout, lake chub, and slimy sculpin, are found as relict populations in spring areas of northeastern Iowa and along the upper Mississippi River in Minnesota (Hubbs and Lagler, 1958). These species may have used the Wisconsin driftless area as a refuge. Only the widespread lake chub seems to have moved westward from the refuge. The brook trout with ecological requirements similar to grayling is not indigenous west of this area. Evermann and Cox (1896) noted the absence of salmonines and other clearwater fishes from western tributaries of the Missouri River and suggested that the shallow, muddy character of the lower reaches may have kept them out. The native fish fauna of the Black Hills of South Dakota was almost entirely catfishes, suckers, and cyprinids, all species that can withstand turbid lowland conditions (Evermann and Cox, 1896). However, it would have been through these lower reaches that a species such as grayling would have had to move when traveling from a Mississippi refuge to the upper Missouri River. Distribution of brook trout is such that reinvasion may have been mainly from the Atlantic slope instead of through the areas occupied by the Minnesota and Ohio relict populations. The brook trout had access northward through glacial outlets of the Great Lakes and Lake Agassiz. They are not found in Lake Agassiz drainages but appear to have recently moved into southwestern Hudson Bay streams from the bay rather than from inland. In the Nelson River, Manitoba, the brook trout migrates up the river to spawn but spends a large part of its life in Hudson Bay; it is found upstream only to the first barrier (Doan, 1948). This may be an ecological as well as a physical block, for the river is fairly warm after leaving the Lake Winnipeg complex and is cooled by springs and tributaries in the lower river. Introductions in the Saskatchewan River drainage have failed except in the foothills of the Rocky Mountains and near Hudson Bay

(Rawson, 1947a).

The failure of grayling to expand its range postglacially along the retreating ice front may be similar to the possible failure of brook trout to spread naturally in the upper Mississippi River.

If we admit that grayling would not find glacial outwash waters to be good habitat, it is difficult to accept that Montana and Michigan populations came from the same refuge, for one or the other would have had to travel several thousand miles. It is doubtful if the Missouri River has ever postglacially been a clear river. Vincent (1962) discussed the possibility of lake trout being indigenous to the upper Missouri River drainage. With both lake trout and grayling found in this area, a glacial refuge in a Pleistocene lake is suggested. Flint (1957) listed 9000 to 10,000 feet as the altitude of the cirque floors in the upper Missouri River area. Scattered glacial cirques were 2000 to 3000 feet above the 400-square-mile Pleistocene lake in Centennial Valley. Glacial Centennial Lake was not formed by ice, so it probably existed for a considerable time. Its small drainage area and limited glaciers would not cause a heavily silt-ladened environment. It would seem that conditions could have been suitable for habitation by clear-water fishes.

Until the Kansan or Illinoian glacial stages, the upper Missouri and Yellowstone rivers flowed northeastward into Hudson Bay (Howard, 1960; Menely _et al_., 1957). In the Sangamon interglacial and early Wisconsin stage, the Missouri River drainage was presumably much as it is now. During the latter stage large temporary lakes were formed in the valleys of southern tributaries flowing along the ice front to the Missouri River. Terminal moraine at the southwestern extremity of the Keewatin sheet dammed the Missouri River at Great Falls forming a lake. Other eastern-slope Rocky Mountain drainages were blocked by ice and morainal deposits. A chain of lakes and connecting drainages extended northward well into Alberta along the corridor between Keewatin and Cordilleran ice, for the Keewatin ice reached its furthest advance after the Cordilleran valley glaciers had retreated (see Alden, 1932). These ice-front lakes were comparatively shortlived and of little value as refuges, but they would have provided temporary avenues of movement from east to west and north to south along the base of the mountains.

Löve (1959) discussed a fluctuating corridor that existed along the eastern slope of the Rocky Mountains between the ice sheets. Northern conifers are thought to have used this route. To hypothesize that grayling and lake trout moved through this corridor to reach Montana from Alaska seems unreasonable. The fishes would have had to have migrated southward very rapidly while the route was open. Absence of grayling from headwaters of the Saskatchewan River supports this view. However, the apparent presence of a native population of lake trout in Chief Mountain Lake of the upper Saskatchewan River drainage in Glacier National Park suggests the contrary (Vincent, 1962).

Other observations suggest that grayling is a recent arrival in the upper Missouri River fish fauna. It is not found above barriers like the cutthroat trout and has not crossed into the Snake River drainage. The narrow ecological requirements of grayling may restrict movement since it is not a turbulent mountain-stream fish; so perhaps it had access to head waters but the habitat was unsuitable. The absence of grayling from lakes above barriers in which it flourished upon introduction suggests denied access to headwater areas.

Two large areas of localized glaciation, upper Sun River Canyon and Yellowstone Plateau, have probably not been invaded by species over the barriers. The upper Sun River Canyon has no indigenous species. A large escarpment at the canyon mouth has prevented reinvasion, and evidently no headwater capture occurred postglacially. The four species native to the Yellowstone Plateau, cutthroat trout, longnose sucker, longnose dace, and mottled sculpin, have probably reoccupied the area postglacially from the Snake River drainage. It thus appears that it may take a longer time than has passed since ice retreat for some species to occupy headwater areas above barriers. Those species widely distributed above barriers must have inhabited the drainage before the last ice retreat. Quaternary fault scarps and tilting are common throughout much of the upper Missouri River area (Myers and Hamilton, 1961) and may account for some stream barriers.

Three eastern fishes of the grayling community, longnose sucker, longnose dace, and mottled sculpin, have crossed westward into the Snake River drainage probably by Two-Ocean Pass. Three other species, cutthroat trout, mountain whitefish, and mountain sucker, have moved eastward from the Snake River drainage to the Missouri River drainage. This route has apparently been open for a long period to allow this exchange. However, grayling, owing to ecological, geographical, or time restrictions, has not crossed the pass.

The grayling populations of Michigan and Montana were restricted to small areas for a long time. Since the last glaciation, habitat within the range was remarkably uniform and stable. Mutation and natural selection for a varied gene pool were limited. Selection and inbreeding in such a small homogeneous population tended to reduce heritable variation and encourage homozygosity. Genes tend to become fixed in the entire population or to be lost (Sewall Wright Effect, Wright, 1931). Population genotypes are limited, and traits that appear to be non-adaptive may be prominent.

A population's nongenetic physiologic response to environmental change can take place only if the pre-existing genetic base includes this reaction. This type of adjustment may respond comparatively rapidly providing that the much slower-formed genetic base exists. An organism without a broad genotype has a limited immediate adaptive capacity.

An organism must maintain its ecological position after it has once evolved to fit a particular habitat. Frequently, the organism reaches a cul-de-sac in which it is well adapted for the existing environment but lacks a varied genotype enabling it to adapt to changing conditions.

High population densities indicate that grayling was well adapted to its environment. Failure to survive in modified habitats and when introduced into other waters suggests a genetically uniform population. Those waters in which grayling introductions have succeeded were nearly always alpine lakes with specific physical and biological features.

The grayling population in the Otter River, Michigan, lived in a more diverse community and under a more fluctuating environment than other southern populations. It is impossible to do more than surmise the role of a diverse ecosystem upon the grayling persisting in this river.

From the foregoing we can summarize that taxonomic relationships of southern populations to each other and to themselves are unclear except that all are similar in many ways. The two southern populations probably spent the last glaciation south of the ice front and probably also in different refuges. Each population is along the southern border of a biome where climatic fluctuations would be manifested. The grayling is typically a member of a community that contains few other fish species. It almost appears as if grayling is an anomaly in regard to the other community members. The grayling is neither a lowland species nor a headwater species as are many of its associates. It would be expected that members of these isolated populations would have a narrow genetic base, thus limiting nongenetic adaptation. In general, a warming period following Wisconsin glaciation is causing less favorable environments for cold stenothermic species.

GRAYLING HABITAT

Within all of their nearly circumpolar range, the graylings have a sporadic and irregular distribution. Adjacent streams may or may not support a population. Immediately, a specificity of habitat is suggested. The graylings have a narrow ecological amplitude that limits their distribution to certain streams or certain sections of streams. In Europe the longitudinal stream section occupied by grayling is so specific that it is named the Grayling Zone.

True, the graylings are found in a variety of environments: Great Britian, Alps, across arctic tundras, 7000-feet altitude in Montana, and only a few hundred feet in Michigan. They live in small alpine lakes and in lakes as large as Lake Baikal. Essentially, along the southern border of their range, they are a mountain- or foothill-type fish.

Characteristics of Grayling Habitat

Since the grayling in North America is often associated with alpine, arctic, or subarctic conditions, misconceptions have arisen concerning its optimum habitat. It has been presumed that swift mountain streams and very cold temperatures are required. This is not so as will be seen in the following discussion of habitat requirements.

Water source

In high latitudes arctic grayling has adapted to turbid meltwaters by migrating between the larger streams, which fluctuate greatly and become silt-laden during late spring and summer, and stable, small clearwater tributaries and lakes. Then in fall and winter, as severe icing begins in the tributaries, it returns to the now-clear main rivers (Elrod, 1931; Ward, 1951; Wojcik, 1955; Wynne-Edwards, 1947b). Air temperatures in high latitudes are low enough so that water temperatures do not become overly warm. Occasionally arctic grayling is found in muskeg brown-water-type streams (Ward, 1951). The southern grayling is almost always associated with spring-fed streams. Michigan's central plateau is mainly a coarse glacial sand that filters precipitation, yielding a cool, even water flow to streams through springs and seepage. Many small tributaries in the grayling region of Montana are also spring fed. In fact, it is from these small streams that early records of concentrations of the fish originated (Elk Springs Creek, O'Dell Creek, Meadow Creek, Horsethief Springs Creek, the many eastern tributaries of the East Gallatin River.) At Georgetown Lake, Montana, where the southern grayling flourished following introduction, spawning took place in a spring-fed tributary. The main similar character of lowland grayling streams in Europe is that they are spring fed (Schumann, 1958). Two features in particular mark spring-fed streams, stability of temperature and of flow.

Water temperature

The relationship between fish distribution and water temperature is complex. Such factors as thermal history, stage in life cycle, length of exposure, availability of cooler or warmer water have to be considered. Thus, for graylings the range of temperature tolerance in nature is wide but generally between 50 and 65° F. This is not much different than that frequented by trouts. Although properly classified as a coldwater fish, there are indications that southern grayling may survive best with a summer maximum above 55° F. Dean (1913) and Metcalf (1961) believed that the Michigan grayling thrived in warmer water than brook trout. In 1879 Metcalf had success holding adults and hatching eggs of southern grayling at 60° F. Lord (1932) had good hatching success at 59.6° F., and tolerance of adults to pond water was up to 74° F. Mr. Harry Baker, manager of the U.S. Fish and Wildlife Service hatchery at Ennis, Montana, believes that grayling will tend to avoid water temperatures below 50° F.

Elk Springs Creek, Montana, where grayling was very abundant, has a nearly constant temperature of approximately 58° F. Nearby, Culver Springs has a temperature of 41° F. (Banko, 1960), but the ponds immediately below warm the water to about 47° F. Early accounts do not mention the outflow of Culver Springs as an important grayling stream. Horsethief Springs on the Madison River had a temperature of 48 to 50° F. on August 24, 1891 (Evermann, 1893). The upper Madison River usually has water temperatures in the 60's and low 70's (Benson _et al_., 1959); however, in 1960 a maximum of 81° F. was recorded (Heaton, 1961). Below Quake Lake water temperatures reached 78° F., and below Meadow Lake, 80° F. As the Madison River was a major grayling stream, the 30° F. difference between Horsethief Springs and the main river suggests that the fish may have stayed in cool, spring-fed tributaries during the time of late-summer high water temperatures.

Grayling waters in Michigan apparently had maximum temperatures between 50 and 60° F. (Hallock, 1873a; Harris, 1884; Henshall, 1900), not unlike the temperatures of those in the European foothills (Schumann, 1958).

In subarctic streams a lower maximum temperature may be required. In Alaska Wojcik (1955) observed arctic grayling to show discomfort at 63° F., and at 68° F. to move to cool inlet streams.

Freezing

The tempering of water temperatures by ground water makes freezing unusual in many segments of grayling water. Mather (1874) and Norris (1879) noticed that spring areas on the rivers of Michigan were ice free. During recent winters solid ice has not formed on the Au Sable or Manistee rivers. In Montana the upper Madison River, O'Dell Creek near Ennis, and Elk Springs Creek do not usually freeze (Banko, 1960). One of Alaska's best-known grayling streams, Big Delta Clearwater, never completely freezes (Wojcik, 1955).

Stream flow fluctuation

Streams that are fed largely by springs or seepage tend to have more stable volumes of flow than ones that are fed largely by runoff. Streams of Michigan flowing over the sandy plateau of the northern half of the Lower Peninsula have least seasonal fluctuation in water flow. The Manistee River is one of the most stable in the United States with a maximum flow of less than twice its minimum (Wisler and Brater, 1959). A slight rise during snow-melt when the ground is still frozen and impervious is usually the major annual upward fluctuation. In other seasons the porous soil nearly eliminates surface runoff.

Montana streams, in contrast, have a peak flow between mid-May and mid-July. Where irrigation is not too demanding, these flood and low flows are minimized by snow-melt that continues at progressively higher elevations throughout the summer. In northern Canada numerous lakes, oxbows, and bogs function as delaying reservoirs to stabilize stream flows. In northern Canada and Alaska grayling moves into the smaller, more even-flowing tributaries during late-summer peak flows. This may have also been the situation in Montana. If grayling migrated into smaller spring-fed tributaries for spawning, they would not be in main rivers during most of the high-flow period.

Water current

One of the most noticeable features of grayling habitat is its intermediacy between dashing and sluggish streams. Streams of Michigan that were inhabited by grayling all had a gradient of from 4 to 10 feet per mile and streams of Montana, up to 20 feet per mile. Often though, in the West, areas of grayling concentration were sections of streams in mountain valleys where the gradient gave a flow of approximately 1 to 2 feet per second which is similar to that of grayling zones of European-foothill streams (Schumann, 1958) and Big Delta Clearwater in Alaska (Wojcik, 1955). Phrases used to describe grayling waters are: "lower reaches of long, deep waters" (Harris, 1884); "gentle current" (Hallock, 1873b); "deep runs at ends of pools" (Harris, 1904); "current with gliding, sliding motion" (Northrup, 1880); and "smooth, steady current" (Norris, 1879). Lowe (Taylor, 1954) described the grayling area of the Otter River, Michigan, as having a moderate current and averaging 2 1/2 feet in depth. Rapids and white water are rare with the water surface usually unbroken. Flow tends to be more laminar than turbulent. As this type of stream seldom occurs, much grayling habitat is occasional holes and riffles separated by long runs.

Bottom

A coarse-sand and fine-gravel bottom is usually found in grayling streams. In Michigan firm, coarse sand was most common with scattered gravel or gravel bars (Hallock, 1875 and 1888; Harris, 1892; Herrick, 1926; Kendall, 1915; Mather, 1874; Rough, 1887). Outside of Michigan a substrate of larger particles was common; it was used especially for spawning, as follows: Montana, gravel and coarse sand (Kruse, 1959; Nelson, 1954); Saskatchewan, 1/2 to 1-inch gravel (Ward, 1951); Europe, sand or gravel (Seeley, 1886); Sweden, gravel of less than 1/2-inch diameter (Fabricius and Gustafson, 1955). The bottom material used by graylings for spawning appears to be of smaller diameter particle than that utilized by trouts.

Water depth

The grayling is or was seldom found in water over 5 feet in depth. It did not frequent deep, still holes (Northrup, 1880) and it avoided shallow riffles (Harris, 1887 and 1904) except for spawning (Kruse, 1959). In Canada and Alaska, grayling may move into deep holes or beaver impoundments to spend the winter (Schumann, 1958; Ward, 1951).

Silt

Grayling streams carry little silt (Bissell, 1890; Henshall, 1907; Richardson, 1836; Ward, 1951; Wojcik, 1955). When muddy water is common during parts of the year, the grayling usually migrates into clear-water tributaries. This fish is seldom abundant in main arctic rivers, which are usually muddy, but it may be very abundant in small, clear tributaries (Elrod, 1931). Silt from the large streams in Alaska may force grayling into the tributaries during much of the summer (Wojcik, 1955).

Aquatic vegetation

Many grayling streams have had abundant aquatic vegetation. Some observers mistakenly believed that grayling spawn was deposited on vegetation, so commonly were the two associated (Kelley, 1931). In Michigan, patches of vegetation were common in the Jordan (Harris, 1884) and Manistee rivers (Hallock, 1875). In Montana, sections of rivers (Madison River, Elk Springs Creek, Horsethief Springs) have much aquatic vegetation. Schumann (1958) noted that European grayling streams are rich in aquatic vegetation. Grayling rivers in Alaska, however, are usually barren of rooted plants.

Lake habitat

Introduced populations of southern grayling are more common in lakes than streams. Lakes in which grayling do well are usually alpine lakes above agriculture zones, have comparatively shallow basins with relatively wide, sandy littoral areas. The inlet streams used for spawning meander over a small open delta that often forms at the head of alpine lakes. The inlet has eroded to nearly base level and may be only a foot or two wide between steep banks. Bottom material is coarse sand and fine gravel. A fairly constant water flow is from springs, snow-melt, and seepage. Water temperatures may become warm in shallows for short periods, but because of the high altitude, water temperatures above 70° F. are rare. Grebe Lake in Yellowstone National Park is a typical example of an alpine grayling lake. Lakes that have grayling in Glacier National Park, Washington, Utah, Wyoming, and Colorado are all of the same nature.

In northern Canada grayling is found often along rocky-sandy shores of the larger lakes (Miller, 1947; Rawson, 1947b and 1951). Few grayling move into the open waters but tend to remain near shore, in bays, or near stream mouths (Miller, 1947). Gill netting in Great Slave Lake captured no grayling below 20 to 30 feet (Rawson, 1951).

Discussion

The grayling is specific in habitat requirements. Areas south of the subarctic that provide suitable conditions are few and scattered. The two widely separated southern populations probably occupied the largest available areas that provide this habitat south of Canada.

Typical grayling habitat

From the foregoing information we can portray a hypothetical grayling stream. Its source will be a spring or other constant supply. Water temperatures will range mostly from 50 to 65° F. Flow will have little fluctuation and will be free of silt. Prevaling water velocity will be from 1 to 2 feet per second in a stream gradient between 5 and 15 feet per mile. The stream bottom will be mainly coarse sand and fine gravel, especially where spawning takes place. Water depth is 1 to 3 feet and beds of aquatic vegetation are common.

Horsethief Springs as an example of grayling habitat and of habitat destruction

Horsethief Springs, Montana, a small tributary to the upper Madison River now flooded by Hebgen Lake, is an example of good grayling habitat that was destroyed by man.

Jordan in 1889 (1891) received reports from one of his expedition members of the abundance of grayling, cutthroat trout, and whitefish in this stream. In 1891 Evermann (1893) wrote that probably no place in Montana are the foregoing fishes more abundant. Henshall (trip rept. at Bozeman Station, Oct. 31-Nov. 9, 1897) found Horsethief Springs "full of grayling, whitefish, and many cutthroat trout."

As these springs were considered a possible water source for a fish hatchery, Evermann (1893) described the area in detail. Two spring areas flowed together to form a 1 1/2-mile-long creek that meandered across a level meadow to join the Madison River. The current was 1 to 2 feet per second; width, approximately 70 feet; and water depth, 5 to 10 inches. The upper section had a bottom of pea-sized gravel and the lower section, a white sand bottom. This lower section was nearly filled with aquatic plant growth: algae, moss, grass, etc. The water was reported never to freeze. Water temperature on August 24, 1891, was 48 to 50° F. The grayling was mentioned as being present in August, October, November, and December; since this is not the spawning season, it seems probable that the population was resident.

In March, 1899 (letter at Bozeman Station), Horsethief Springs was nearly devoid of grayling. Only a few individuals were present in the short north-branch section above its confluence with the south-branch spring. The reason for this decline was that manure washing from a recently constructed barn polluted the water. Artificial Hebgen Lake then flooded the spring area in 1915 and wiped out the remainder of the stream habitat.

These two disturbances are the type of conflict grayling has frequently encountered. That Horsethief Springs was good habitat can hardly be questioned. This same level meadow with a clean, year-around water supply was ideal for a rancher's barn, and wide openings in a valley of this type were often the first to be utilized for water storage.

Horsethief Springs is an example of man choosing the small meadows, required by grayling, for areas of his own use and development.

Topographic features where grayling habitat occurs

Essentially, if given the proper water source and climate, stream gradient will determine the habitat. Thus, within the confines of the two areas of southern populations, the irregular distribution pattern is determined by stream gradient. In central Michigan the topography is such that nearly all streams qualify. In the Upper Peninsula those streams in the eastern part are too low of a gradient, and those on the west, too steep. The Otter River is one of the few streams that is intermediate. In Montana the upper Missouri River drainage pattern is of a two-story nature. A medium gradient area adjoins the Missouri River Valley, then a steep canyon area, and on the high plateaus the gradient lessens again. Small mountain valleys may have suitable slope within the canyons. The lower Sun River and lower Gallatin Valley are examples of grayling habitat on the main valley floor. The upper Smith River, tributaries of the upper Gallatin River, the Big Hole River, and the upper Madison River are examples of medium slope at a higher elevation. Small valleys are represented by Sheep Creek, a tributary of Smith River, and the section of Madison River Valley now inundated by Hebgen Reservoir.

Much arctic and subarctic topography is such that rivers are potential grayling habitat. Arctic rivers typically have even profiles with remarkably few rapids or falls; normal water flow is about 3 miles per hour (approximately 4.5 feet per second), and lakes acting as settling basins reduce turbidity over long sections of stream (Wynne-Edwards, 1952).

Water velocity is one of the most important ecological stream characters. The nature of the stream bottom, amount of silt, abundance of aquatic food organisms, and many other features of a stream ecosystem may be governed by current velocity. Thompson and Hunt (1930) found that headwater species usually had a wide ecological tolerance and were found throughout the stream, but that other species were restricted to their respective sections. In western and central Europe there are numerous areas where the ichthyofauna relates to stream gradient (Starmach, 1956). Burton and Odum (1945), Trautman (1942), and other American workers have found a correlation between fish distribution and stream gradient. A certain velocity may be required at only one stage in a fish's life history. For example, kokanee salmon in California would spawn in water velocities below 2.15 feet per second but avoid velocities over 2.19 feet per second (Delisle, 1962). After an exhaustive study of the Elbe River, Germany, Kothé (1961) concluded that changes in the aquatic flora and fauna were due mainly to changes in water quantity and morphological structure of the river, not by changes in water quality as is often assumed. That local distribution of grayling is chiefly controlled by stream gradient is not surprising. The topographic and climatic relationship over southern Canada and the United States is such that few areas of grayling habitat exist.

Of course, other factors besides physical environment influence grayling distribution. There are few streams in the United States that meet grayling habitat requirements and, as will be discussed later, most of these streams have been greatly altered by land use.

EFFECT OF GRAYLING EXPLOITATION

The history of grayling includes a period of heavy exploitation that may have been a significant factor in local decline or demise. Opening of hinterlands by the advent of railroads was at least partly responsible for this in both Michigan and Montana. Many studies, including theoretical ones (Beverton and Holt, 1957; Ricker, 1958), have been concerned with the influence of exploitation on population levels. Actual effects of overexploitation are poorly studied. The general contention is that fish populations are seldom, if ever, endangered by extermination through fishing. McFadden (1961) separated the reasoning behind this idea into three concepts: (1) fish become difficult to catch at low-population densities, (2) fishermen lose interest at low-fish population densities, and (3) high-fishermen concentration discourages additional fishing.

Ease of Capture and Early Catches

Throughout its range the American grayling was and still is very susceptible to angling. It is one of the easiest fishes to catch. Representative reports are that it is not readily frightened by boat or fisherman (Norris, 1879; Brown, 1938b); nearly all grayling may be taken from a pool (Henshall, 1900); and even an inexperienced fishermen has little difficulty making large catches (Northrup, 1880).

Adults of the grayling feed vigorously and almost without caution. While fishing Agnes Lake in Montana, I succeeded in coaxing what was apparently the same fish to rise eleven times to an artificial fly. Such persistence is not unusual. Roger Reed (pers. comm.) made use of college students who had fished little or not at all to catch a series of grayling in Alaska. These students caught and tagged an average of five fish per hour; one student caught and tagged 337 grayling in one day.

Early grayling exploitation by white man resulted in enormous individual catches: three men caught 600 pounds of grayling in two days (Furman, 1878); 47 were taken from one pool (Henshall, 1900); two men and two ladies caught 3000 in two weeks (Mich. Sports Assoc., 1879); bushel boxes full were captured (Schbarber, pers. interview). Total catch may be exaggerated because of the large size of individual catches by a few fishermen. Annually, some six wagons were filled with grayling at a dam across Hersey Creek, Michigan (Parker, 1888). Catches were as high as 5000 from 5 miles of the North Branch of the Au Sable River (Norris, 1878). If the river averaged 25 feet in width, each mile would be nearly 12 acres of water. The catch would amount to approximately 83 fish (estimated 42 pounds) per acre which, even if the stream were not fished much the remainder of the season, would be a good yield for a coldwater stream. In comparison, fishermen removed from Lawrence Creek, Wisconsin, an annual average of approximately 52 pounds of trout per acre for three years (McFadden, 1961).

Until 1880 a commercial fishery on the Madison River provided fresh fish for the miners in Butte and Virginia City, Montana. In another fishery the hotel and camp companies within Yellowstone National Park were permitted to catch and serve fish to guests up to 1919. The last year of this practice about 7500 pounds of "trout" were served

(Fromm, 1941). Very possibly grayling made up a part of both fisheries. From Michigan, the Chicago and Milwaukee markets utilized all grayling available until about 1885. Sixty pounds was considered an easy day's catch by an experienced commercial grayling fisherman in 1875 (Irland, 1920).

Examples of Possible Overexploitation

Because of synchronous events it is usually difficult to separate the effect of overexploitation from other causes of decline. Two fairly clear examples, one from the Au Sable River and another from the Madison River, may be helpful. Other instances are known, but their interpretation is clouded.

The Au Sable River, Michigan, for which most information is available, was heavily fished for the commercial market (Mather, 1875; Banta, 1876) as well as being the center of early sport fishing. Fishing expeditions started from the village of Grayling, which was the only point of early access to the river. Grayling fishing declined first near the village of Grayling and then, progressively downstream (Figure 4). Fishing expeditions in 1873 (the first major ones) made no mention of the stream immediately below the village of Grayling being void of fish (Hallock, 1873a; Milner, 1873). However, many subsequent fishermen mentioned the increasing distance necessary to go downriver in order to catch fish (Table 3).

Overfishing seems to be the main cause of this decline. Probably more correctly, the decline started by overfishing then continued due to logging activities. Logging did not expand greatly in this region until approximately 1880. The brook trout was not present in

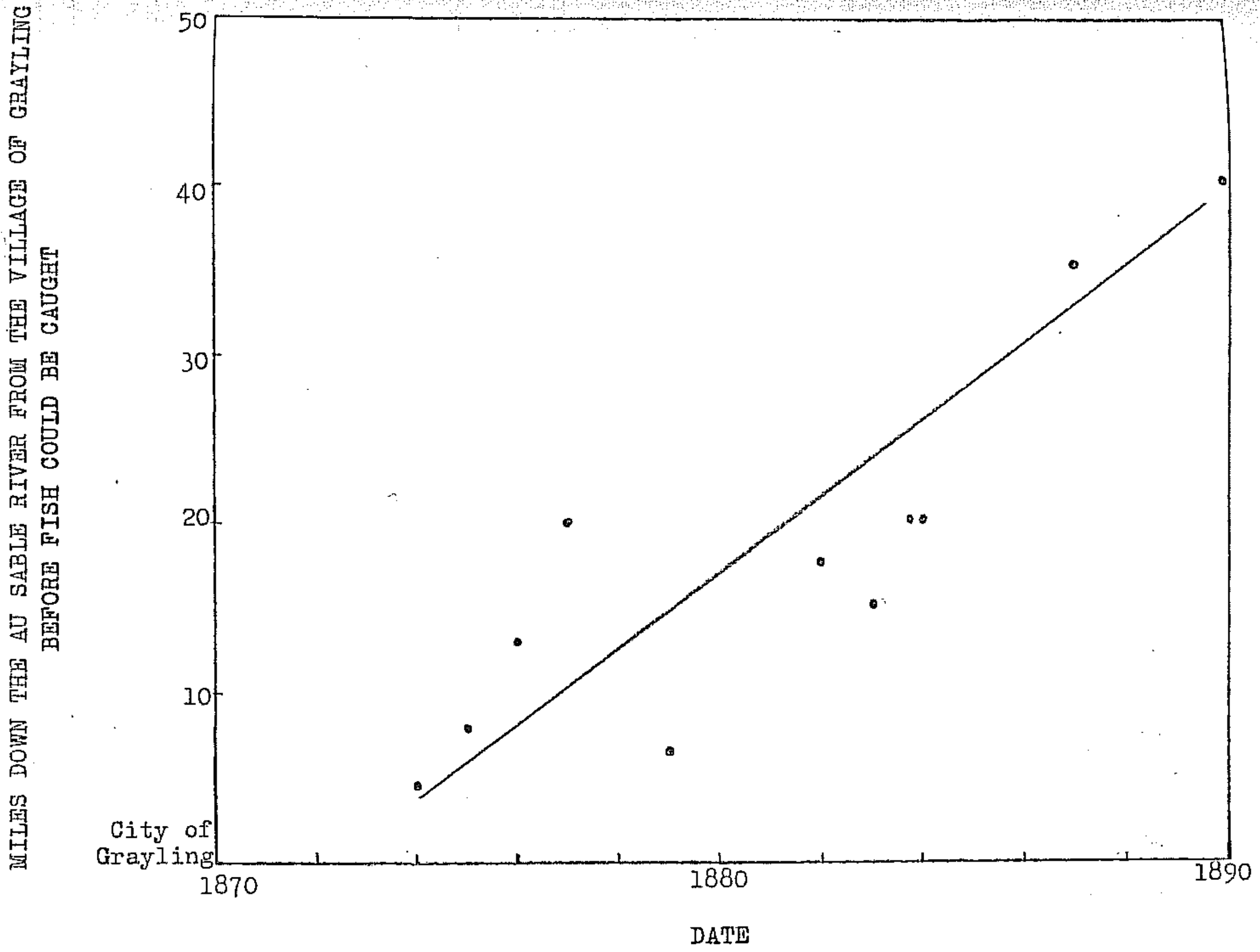

Figure 4.--Grayling decline that began first near the village of Grayling, Michigan, and progressed successively downstream.

TABLE 3.--Records of successive downstream grayling decline in the Au Sable River below Grayling, Michigan

Date	Statement of miles	Authority
March, 1874	Saw many, first days travel of 5 miles	Mather, 1874
May, 1874	Caught 50, first 8 miles	Green, 1874
August, 1874	None for 4-5 miles	Norris, 1879
April, 1875	None for 8 miles	Mather, 1875
--- 1876	12-15 miles downstream to good fishing	Banta, 1876
Sept., 1877	Declining above North Branch for 2 years	Oatka, 1888
August, 1877	None for 20 miles	Norris, 1878
July, 1879	None, first 6-7 miles	Northrup, 1880
--- 1882	Plenty of fish 15-20 miles downstream	G. D., 1882
--- 1883	None for 15 miles	Mich. State Bd. Fish Comm., 1885
Spring, 1884	None for 20 miles	Mich. State Bd. Fish Comm., 1885
--- 1884	Good fishing 20 miles downstream	Anonymous, 1884a
--- 1884	Fishing not as good a few miles downstream as used to be	Anonymous, 1884b
--- 1887	Have to go 30-40 miles downstream for fishing	Bebe, 1887
--- 1890	Have to go 40 miles for good fishing	Shields, 1892

large numbers until after 1890 (see following chapters).

By 1910 the fame of Madison River, Montana, for grayling and cutthroat trout fishing was widespread. This river still enjoys the reputation as one of the better trout streams in America; but now its fame is for the introduced brown trout. Mr. Kohles, a former state game warden, said that between 1924 and 1928 fishing pressure was very heavy. He would frequently check as many as 100 fishing licenses at a favored location. It was at this time that access roads were improved and concern was expressed already over the possible undesirable effect of new highways upon Montana fishing (Thompson, 1925).

Montana hunting and fishing license sales from 1905 to 1930 may indicate trends in fishing pressure (Table 4). No resident licenses were required before 1905. From then to 1930 a combination hunting and fishing license was issued after which a separate fishing license was available so the data are not comparable. Plotted on Figure 5, the licenses issued show a general rise paralleling the increase of exotic trouts and an inverse relationship to grayling decline. In this instance possible influence of fishing upon the grayling population cannot be separated from competition with exotic trouts.

The upper Madison River within Yellowstone National Park is one area of past grayling habitat that has probably changed little in historic times. Since the Park was set aside in 1872, agriculture or logging has not taken place. Accounts of the upper river and the countryside in 1889 (Jordan, 1891) and in 1891 (Evermann, 1893) describe it nearly as well today. Changes in the game-fish community would therefore be caused by competition or fishing if we discount effects of gradual climatic change.

TABLE 4.--Total number of Montana fishing and hunting licenses sold between 1905 and 1930. After 1930 fishing and hunting licenses were separated so are therefore not comparable. (From Montana State Fish and Game Commission biennial reports.)

Date	Resident	Non-resident	Total
1905	30,087	83	30,170
1906	---	---	24,410
1911	57,302	1721	59,023
1912	45,322	1152	46,474
1913	64,337	1405	65,742
1914	54,585	999	55,584
1915	---	---	---
1916	69,466	1082	70,548
1917	72,113	1012	73,125
1918	42,744	741	43,485
1919	70,429	252	70,681
1920	52,751	1305	54,056
1921	59,348	1879	61,227
1922	50,508	1620	52,128
1923	64,202	2193	66,395
1924	56,113	2064	58,177
1925	73,042	3369	76,411
1926	71,249	3133	74,382
1927	67,083	3320	70,403
1928	75,063	4335	79,398
1929	83,388	4793	88,181
1930	82,331	4732	87,063

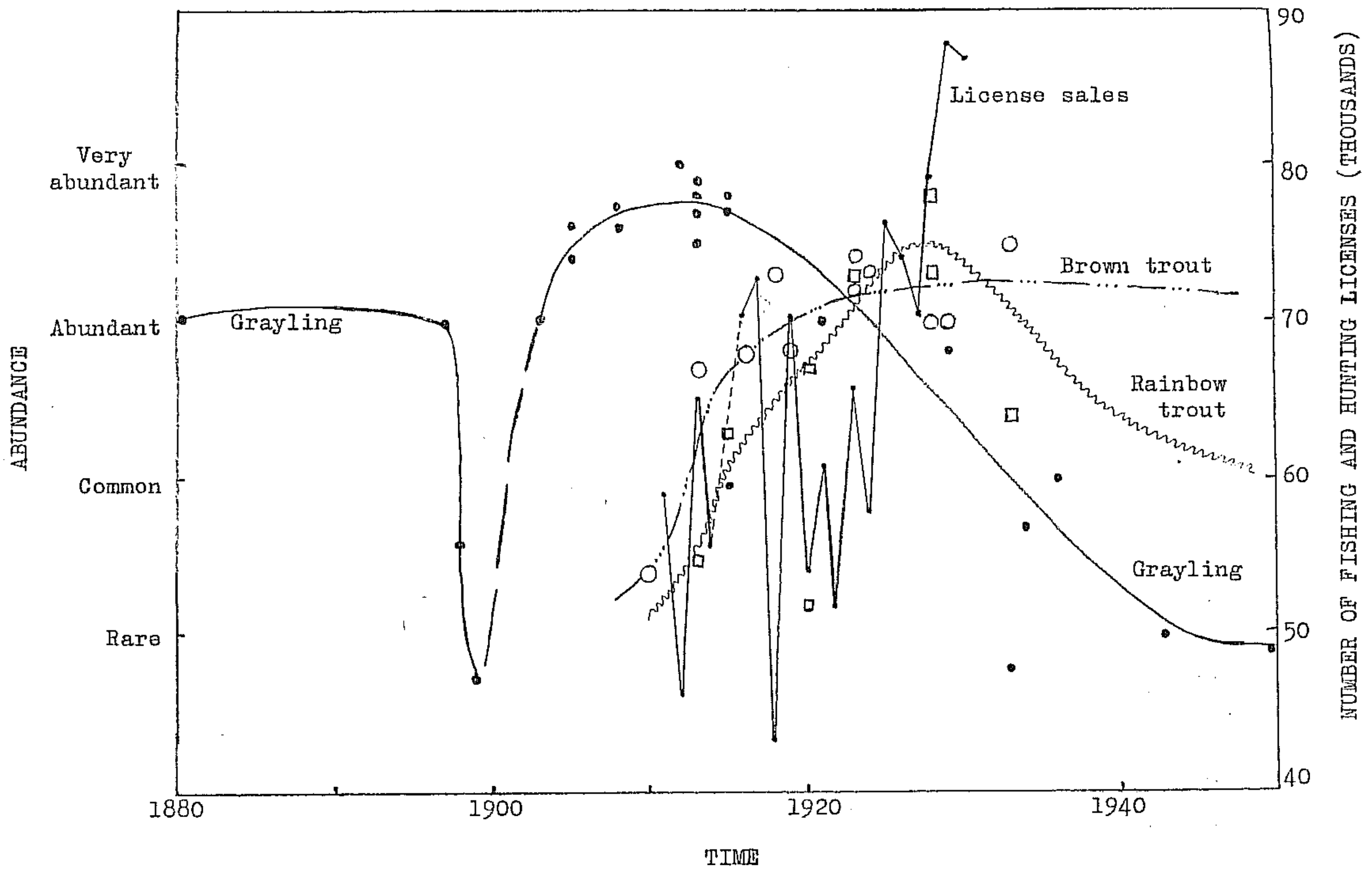

Figure 5.--Changes in the game-fish community of the central Madison River and the number of Montana state hunting and fishing licenses issued.

In Yellowstone Park the major increase in park visitors occurred approximately when grayling declined (Table 5 and Figure 6). The first creel-census study made on the Madison River (years 1953 to 1957) showed a positive relationship between numbers of park visitors and angler hours (Benson et al., 1959). Earlier a similar relationship had been assumed on Grebe Lake in the Park (Moffett, 1950). Fishing pressure in Yellowstone Lake was likewise discerned to be roughly proportional to the annual number of park visitors (Cope, 1957).

Grayling populations remained high in the upper Madison River until about the same time as in the lower river even though exotic fishes were present for nearly twice as long a period in the upper river. In both river sections grayling seemed to decline when fishing pressure was increasing regardless of the period of competition. Since there was some habitat change in the lower but not in the upper river, this may have been an additional adverse factor.

Discussion

When other game fishes are present in a grayling community, differential response to angling operates against grayling, especially if other members include such relatively more-difficult-to-catch brook, brown, or rainbow trouts. Angling is a highly selective process with vulnerability to lures a genetic variable (Manges, 1951; Miller, 1957). The accepted ranking of trout vulnerability from most to least difficult to catch in daytime fishing is brown trout, rainbow trout, and brook trout (Thorpe et al., 1947). How this may function among trouts in a community was indicated by Cooper (1952a) who showed that three brook trout were caught for each one remaining in a stream section at

TABLE 5.--Annual number of visitors to Yellowstone National Park.

Date	No. of visitors
1904	13,727
1905	26,188
1906	17,182
1907	16,414
1908	19,572
1909	32,545
1910	19,575
1911	23,054
1912	22,970
1913	24,929
1914	20,250
1915	51,895
1916	35,849
1917	35,400
1918	21,275
1919	62,261
1920	79,777
1921	81,651
1922	98,223
1923	138,342
1924	144,158
1925	154,282
1926	187,807
1927	200,825
1928	230,984
1929	260,697
1930	227,901
1931	221,248
1932	157,624
1933	161,938
1934	260,775
1935	317,998
1936	432,570
1937	499,242
1938	466,185
1939	487,936
1940	526,437
1941	579,696
1942	185,746
1943	61,696
1944	86,593
1945	189,264
1946	807,917
1947	937,776
1948	1,018,279
1949	1,131,159
1950	1,110,524
1951	1,163,894
1952	1,350,294
1953	1,326,858
1954	1,329,000
1955	1,369,000
1956	1,114,000
1957	1,596,000
1958	1,442,000
1959	1,409,000
1960	1,443,000

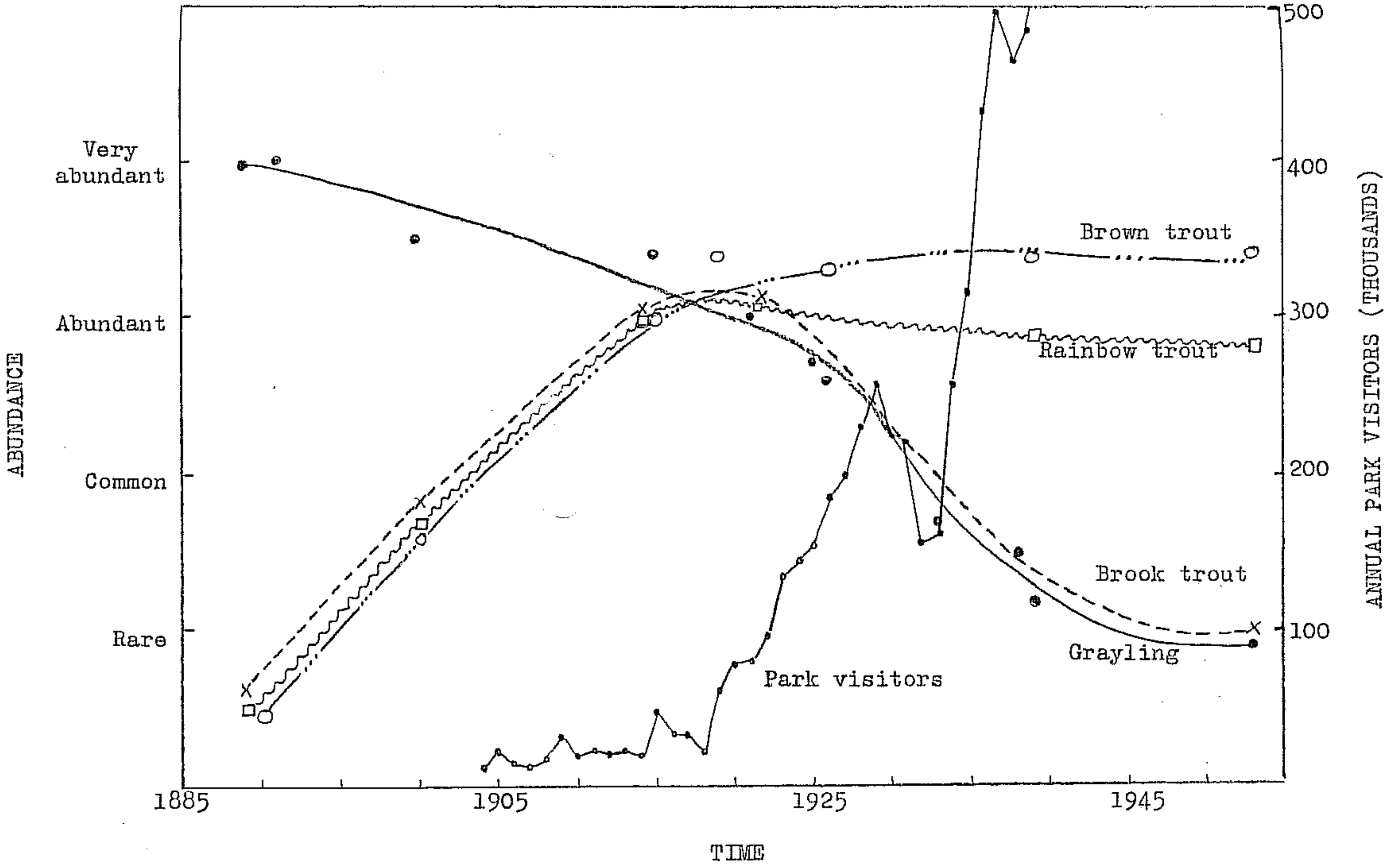

Figure 6.--Changes in the game-fish community of the Madison River in Yellowstone National Park and the annual number of park visitors.

the end of the season, whereas one brown trout was caught for every three remaining. From what was written previously, the grayling may be nearly twice as easy to catch as brook trout and five or six times as easy as brown trout.

Member species of the upper Madison River game-fish community were not rearranged to their present abundance until fishing pressure became high (Figure 7). Concern for the effect of and the possible role of heavy fishing on trout decline has been expressed by Benson _et al_. (1959), Cope (1957), and Wicklund and Dean (1957).

Continued differential predation, including angling, reduces the reproductive capacity of a population. For example, in the Madison River brown trout matured at two and three years of age (Brown and Kamp, 1943), but the catch was mainly three- and four-year-olds (Benson _et al_., 1959). Therefore, the species had ample opportunity to reproduce. In contrast, the catch of rainbow trout in the same stream was mainly two-year-old fish that had not yet spawned. The rainbow trout was at an obvious reproductive disadvantage. It could be hypothesized that a similar disadvantage struck grayling at the time when trouts were introduced into the Madison River. Ease of capture and late maturity of grayling undoubtedly enabled the removal of a large share of the individuals of the species before maturity.

An exception to grayling being selectively caught was noted by Kruse (1959) in Grebe Lake. Fishermen were catching a lower percentage of the grayling than of the rainbow-cutthroat hybrid population. The selection was willful on the part of fishermen who preferred the hybrids and fished for them.

There are exceptions to the expectation that angler interest

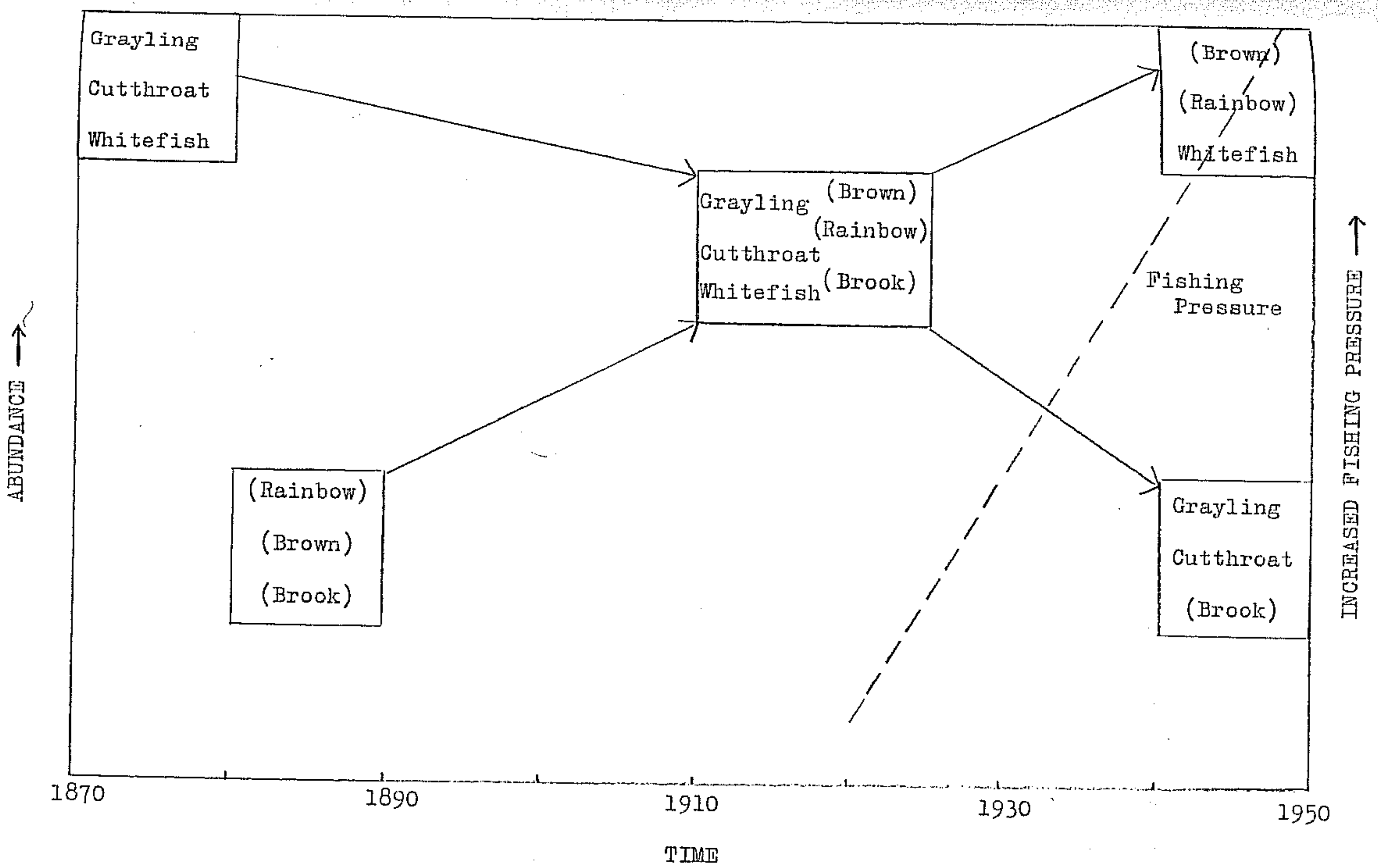

Figure 7.--Hypothetical changes in the game-fish community and fishing pressure in the upper Madison River, Montana (introduced species are given in parentheses).

may wane when the population of a preferred fish reaches a low level. This was experienced for brook trout by McFadden (1961). A similar situation may have pressed grayling to dangerously low levels in stream after stream in Michigan and also possibly in Montana.

The percentage of a population that can be removed without reducing future generations varies according to the species and its environment. No one knows what the critical level may have been for grayling in the two southern populations. Sillman and Gutsell (1957) found that the removal of 75 per cent of an experimental guppy (_Lebistes reticulotus_) population was catastrophic. McFadden (1961) found no reduction in recruitment in brook trout as the result of brood stock depletion by angling over three years at removal rates of 32.2, 59.0, and 64.6 per cent. He attributed population maintenance at this level of severe exploitation to early attainment of maturity.

A hypothetical model may be suggested to illustrate the effect of differential angling. Assume existence of a game-fish community that had 300 each of brown, rainbow, and brook trouts, and of grayling. Furthermore, assume that brown trout and grayling mature at 10 inches in length, rainbow trout, at 8 inches, and brook trout, at 6 inches. It seems reasonable to estimate that for each brown caught, two rainbow, three brook, and five grayling would also be removed. If enough fishing pressure were applied to remove 50 brown trout, the community would then consist of 250 brown trout, 200 rainbow trout, 150 brook trout, and 50 grayling. Under an 8-inch-minimum size, a high percentage of the largest members of the population would be removed first so it could be possible for the 50 remaining grayling to be immature. Recruitment into the brown trout population would not be affected, as only a few of the individuals over ten inches would be removed. The brook trout, although heavily exploited, maintained itself because most individuals could spawn before capture.

In Alaska overfishing is held to be the primary cause of grayling decline in the Fairbanks area (Wojcik, 1955). Here grayling does not mature until five or six years of age, so many individuals are subject to a fishery before reproduction is possible. The deterioration of grayling fishing along the Alaska Highway has also been attributed to overexploitation.

It is therefore apparent that a species so susceptible to a fishery can be subjected to severe selective angling mortality. Under certain conditions it may even be possible to reduce the population below a recovery level. Perhaps the most critical of these conditions are the associated fish species (see section on competition).

In the United States grayling is now caught by so few fishermen that many fail to recognize its identity. In Montana grayling is often misidentified as the unwanted mountain whitefish and discarded on the bank or shore. Many Utah anglers regard grayling as a non-game species, much preferring to catch trout (pers. comm., Phil Dotson). Perhaps it has been the scarcity and an artificial aureole that attracted anglers to grayling. In England grayling is also generally classified as coarse fish and as inferior to salmon and trouts for food or sport (Torbett, 1961). The low esteem with which grayling is looked upon in Great Britian is shown by the following from Coston et al. (1936, p. 174): "Remember that all coarse fish, particularly chub and grayling, are serious competitors of trout in the matter of food."

The grayling of Lake Baikal supports a modest commercial fishery of approximately 200 to 700 tons per year. Angling and set nets are used to make the catch (Nikolskii, 1957). The grayling in many lakes and streams in Sweden also has a commercial fishery (Fabricius and Gustafson, 1955).

COMPETITION FROM OTHER FISHES

Exotic trouts were early introduced into grayling waters. In some streams grayling populations were already low; in others they were still high. In nearly all grayling streams, exotic trouts flourished and grayling declined.

Accepting Clements and Shelford's (1939) definition that competition is a demand by two or more organisms for the same resources or conditions in excess of immediate supply and realizing the validity of Gause's Rule (Gause, 1934), which states that an ecological niche cannot be occupied simultaneously and completely by a stable population of more than one species, it is apparent that trout introduction into grayling communities would necessitate community adjustment. As trouts and grayling are in many ways ecological equivalents, when the introduced population reaches a high enough density both species would be utilizing the same environmental resources. The eventuality that one of the species will become extinct is shown by Frank (1957), Gause (1934), Park (1948), and others.

Competition may be direct, as active antagonism, or indirect, as a species monopolizing a given resource needed by another. The more closely ecologically related the species, the more intense the competition. Degree of competition changes as environments fluctuate to favor one or the other competitor. Along an environmental gradient whose extremes favor two species, there would theoretically be a point on either side of which each species would be superior (Crombie, 1947).

Competition has been repeatedly suggested as the major cause of grayling decline (Brown, 1938a; Creaser and Creaser, 1935; Henshall, 1916; Thompson, 1925; and others). According to Brown (1943), the absence of competitive trouts seems absolutely essential to grayling survival. In nearly every watershed it is difficult to separate effects of competition from other simultaneous influences. In many places where exotic trouts have been introduced, the grayling has declined, but often other changes were involved.

The Brook Trout in Michigan

The relationship of brook trout and grayling ecology is not fully understood. Spread of brook trout into the grayling streams of Michigan was by both natural and artificial means.

Natural distribution and range extension

The native range of brook trout in lower Michigan is difficult to determine because it is a recent natural invader at least into the northwestern part of the Lower Peninsula, and dispersal from introductions had prevaded nearly all other suitable waters before 1900.

The brook trout was common in Lake Superior (Agassiz, 1850; Suckley, 1874) and it is still so. It occurred naturally above barriers in the Huron Mountains (Hubbs, 1929), and in high isolated lakes of Isle Royale (Hubbs and Lagler, 1949), but was rare in other Great Lakes (Jordan and Evermann, 1911). It is considered as a long-time resident of the Upper Michigan Peninsula. In an 1841 account of a trip from Detroit to the Upper Peninsula, Hubbard (1887, p. 215) wrote the following:

> Unfortunately there is not a trout brook, that is, a stream containing real "brook trout," in the whole [lower] peninsula. The moment the Straits of Mackinaw are crossed the brook trout is found in abundance, in all the rills of the Upper Peninsula.

The abundance of brook trout north of the Straits of Mackinac must have been a sharp contrast to their absence on the south. Lanman (1856) noticed the lack of the species about Mackinac Island but reported an abundance of large trout only a short distance away on the mainland. He continued to mention that brook trout was common in both north- and south-flowing streams of the Upper Peninsula.

Strang (1855) reported that in 1853 brook trout was abundant in certain small streams on the mainland, i.e., the Traverse region, but that most streams did not contain the species, only large numbers of a fish that was unknown to him (perhaps the grayling). Norman (1887) wrote that 30 years ago (1857) the Jordan River was predominately a grayling stream with few trout. Old men living near the Jordan River remembered when they caught one trout to every five grayling and said that trout were unknown until 30 to 40 years ago (approximately 1850) (Metcalf, 1961; Whitaker, 1887). About 1864 (Page, 1884) the Boyne and Jordan rivers contained many grayling and few brook trout. These statements, along with that of Parker (1878) who wrote that brook trout did not exist in the Lower Peninsula 25 years ago (1853), strongly suggest the movement of brook trout from the Upper Peninsula to the Traverse region not too long before the middle of the nineteenth century. By natural range extension, the brook trout apparently inhabited streams from the Boardman River to the Ocqueoc River (Bissell, 1890; Hallock, 1873a and 1875; Mather, 1874; Mershon, 1923). Bower

(1882) thought that the Boardman River was the farthest south that native trout had moved. Since brook trout was extending its range, it is not surprising that the trout may have reached naturally the Manistee River. Through the courtesy of the late George C. Depres, the following article is quoted from the Manistee Times of September 11, 1869:

> Our piscatorial friends around Manistee will be surprised to learn that there are speckled brook trout within a few miles of Manistee. On Friday last Mr. Ruggles with other gentlemen camped at Pine Creek and thought they would like some fish for supper. The first fish caught was a speckled brook trout and being elated with their success they kept on fishing and soon had enough for a good mess. It had been the general opinion of our people and tourists that if they wanted speckled trout they would have to go to the neighborhood of Traverse City to catch them. Pine Creek is 18 miles from Manistee so let us patronize home institutions and catch speckled trout in our own creeks.

The brook trout was thus actively dispersing southward until it became intermingled with introduced populations. There seems little question but that the species was native to the Lower Peninsula, at least to the extent that it was not transplanted there by white men (Jerome, 1874; Michigan State Fish Comm., 1875).

Geologically, recent movement of the brook trout into rivers that originally contained grayling probably accounts for early reports of catching brook trout and grayling from the same stream (Henshall, 1919; Mershon, 1923). These unstable stream communities were in transition and both species were present (Table 6 and Figure 8). The change of the Jordon River, Michigan, from a grayling to a brook trout stream was noticed by Norman (1887), Page (1884), and Whitaker (1887). They agree that it took approximately 30 to 40 years for the shift. That is 20 years for the increase of brook trout and another 20 years

TABLE 6.--Records of grayling and brook trout abundance in the Jordan River, Michigan.

Date	Observation	Authority
1857	Predominately a grayling stream, few trout	Norman, 1887
1860	Many grayling; old timers remember catching one trout to five grayling	Whitaker, 1887
1864	Alive with grayling; brook trout rare	Page, 1884
1866	Caught many grayling and trout from same pool	Norris, 1883
1868	Good grayling fishing	Fitzhugh, 1873
1869	Swarmed with grayling	Bebe, 1887
1871	Saw many grayling	Milner, 1873
1873	Grayling abundant	Henshall, 1919
1875	Caught both trout and grayling, more trout	Hallock, 1875
1877	Trout increase; grayling almost disappeared	Norman, 1887
1879	Caught two grayling, many trout	Bebe, 1887
1879	Ceased to be a grayling stream	Northrup, 1880
1879	Grayling nearly extinct	Mich. State Fish. Comm., 1881
1880	One of Michigan's best known trout streams	Page, 1884
1884	No grayling	Page, 1884
1884	Caught 1000 trout, no grayling	Delta, 1884
1885	Once a grayling stream, now trout, only an occasional grayling	Whitaker, 1887
1887	Grayling gone	Norman, 1887

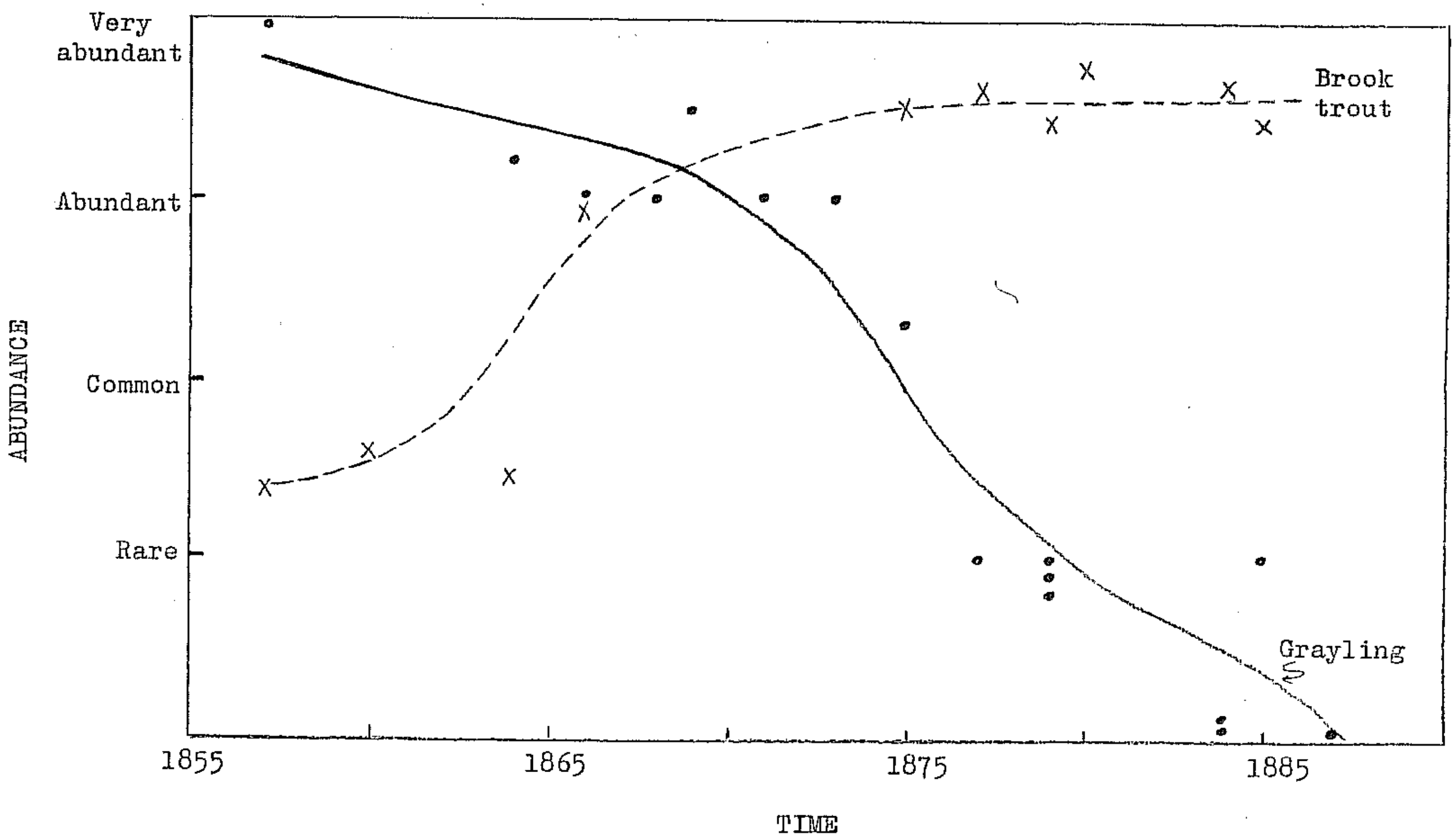

Figure 8.--The change of the game-fish fauna of the Jordan River, Michigan, from dominance by grayling to dominance by brook trout.

for the decline of grayling. A similar pattern existed for the Boardman River (Table 7). Limited information from the Boyne River (Table 8 and Figure 9) shows an abrupt grayling decline at a later date than the Jordan River.

TABLE 7.--Records of grayling and brook trout abundance in the Boardman River, Michigan.

Date	Observation	Authority
1855	One-half trout, one-half grayling	Metcalf, 1961
1867	Trout and grayling together	Anonymous, 1874
1875	Caught 30 trout, 1 grayling	Hallock, 1875
1886	Only an occasional grayling	Whitaker, 1887
1886	Grayling gone	Norman, 1887
1889	Excellent trout stream	Anonymous, 1889

Competition apparently was important in the decline of grayling in streams that had native brook trout populations, or we could say in streams where brook trout were abundant for perhaps 30 years. The decline of grayling in northwestern lower Michigan was underway by 1875, before logging and subsequent habitat change or fishing could have been major factors. Henshall (1916) wrote that Pine Lake-Boyne River waters were an example of competition reducing the grayling population, for the region was not logged until much later. Streams in this area show a pattern of population change similar to that of Madison River, Montana, where grayling decline is nearly coincident with trout increase. In contrast, the decline of grayling in the

TABLE 8.--Records of grayling and brook trout abundance in the Boyne River, Michigan.

Date	Observation	Authority
1855	One-half trout, one-half grayling	Metcalf, 1961
1867	Grayling and trout together	Anonymous, 1874
1870-76	Grayling abundant	Henshall, 1919
1874	Trout and grayling together	Anonymous, 1874
1875	Many trout and some grayling; many trout and 3 grayling	Hallock, 1875
1879	One of Michigan's celebrated trout streams; no mention of grayling	Northrup, 1880
1879	Grayling nearly extinct	Mich. State Fish. Comm., 1881
1883	A brook trout stream	Mich. State Fish Comm., 1885
1884	No grayling; important trout stream	Page, 1884
1886	Good trout stream; grayling almost gone	Whitaker, 1887
1886	Grayling gone	Norman, 1887

Manistee and Au Sable rivers was advanced before trouts were common.

The brook trout did not pervade the Cheboygan River system as rapidly as it had the short rivers in the Traverse region. It was present in large numbers in the short main-stem Cheboygan River in 1874 (Anonymous, 1874; Green, 1874; Mather, 1874). The lakes or their occupants separating the rest of the system may as Whitaker (1887) suggested have acted as a barrier to rapid upstream movement. In 1876 Norman (1887), after a thorough search, found no brook trout in the Sturgeon River nor was it common in 1887 (Bissell, 1890). The

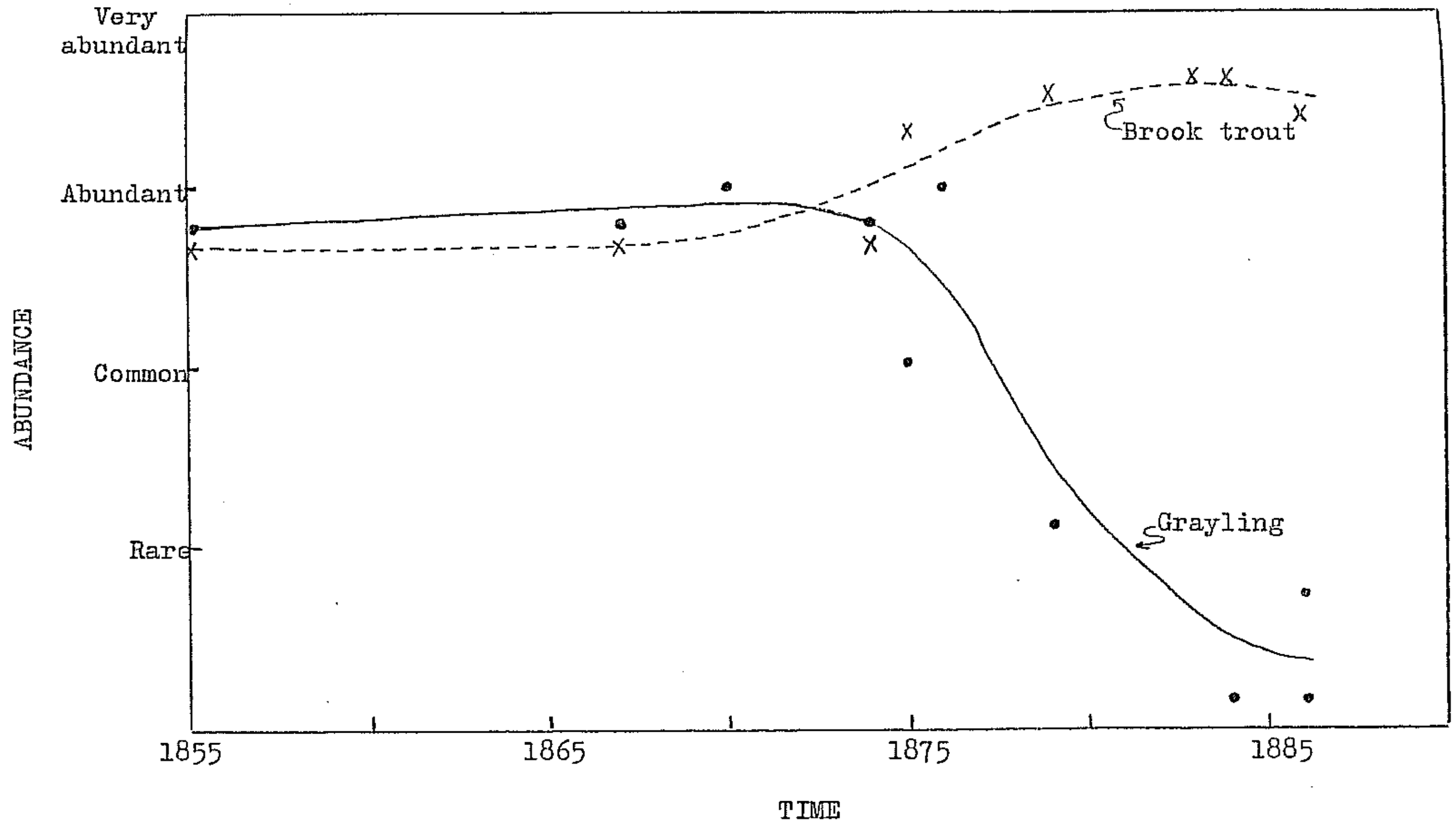

Figure 9.—The change of the game-fish fauna of the Boyne River, Michigan, from grayling and brook trout to predominately brook trout.

brook trout was unreported from the Pigeon and Black rivers until 1884 (Anonymous, 1884c); the Maple River had only grayling in 1885 (Anonymous, 1885b) and had trout and grayling in 1891 (Anonymous, 1897a). Either brook trout was much later in reaching the Cheboygan River or its upstream movement was delayed. The Maple and Black rivers had grayling until 1899 (Hough, 1899) and 1906 (Mershon, 1916), respectively, which was later than most other rivers.

Otter River

The Otter River, at the base of the Keweenaw Peninsula, had a population of grayling until 1934. Since at least 1884 and probably long before (East, 1930), the river contained both grayling and brook trout. This is the only stream in North America where grayling and brook trout coexisted for such a long period and for some of this period grayling did better than brook trout. Lowe (Taylor, 1954) in 1925 found introduced rainbow trout the dominant fish, then grayling, and third, brook trout.

Introduced populations

The first documented introduction of brook trout in Michigan (Mershon, 1923) was in the spring of 1870 in the south branch of the Tobacco River (Clare County). However, in 1866 Mr. Clark of Clarkston (Oakland County) had a private pond that contained this species. No record is available whether he distributed fish to other areas. Early private plantings were made along the Flint and Pere Marquette Railroad in the Hersey, Pere Marquette, Tobacco, and upper Muskegon rivers (Lake, Oscela, and Clare Counties) (Mershon, 1923). In Oceana County the first brook trout came from private stock that was planted in

1878 (E.D.R., 1885).

By 1879 many brook trout had escaped or been planted from private ponds (Mich. State Fish. Comm., 1881). These introduced populations attracted much attention as they were in the southern part of the state where trout had not existed previously. First public plantings were made in Cass, Berrien, and Kalamazoo counties in 1879 (Mich. State Fish. Comm., 1881). Additional introductions in 1880 were in Allegan, Berrien, Cass, Calhoun, Clare, Kalamazoo, Kent, Mecosta, Newaggo, Oceana, Van Buren, Washtenaw, and Wexford counties. Before 1880 the only watersheds containing grayling that had been stocked with brook trout were the Pere Marquette and Muskegon rivers. There is no record of brook trout being planted in the northern part of the Lower Peninsula until 1882 when streams in Cheboygan and Charlevoix counties were stocked (Mich. State Fish. Comm., 1883). Also, at the latter date 3000 brook trout were stocked in the Rifle River so that all of the southern-most grayling streams had now been planted with brook trout.

Letters to the State Fisheries Commission recorded the remarkable success of these early introductions (Mich. State Fish. Comm., 1883). Both growth and reproduction were excellent. This would indicate that probably time was the major factor that had kept the indigenous brook trout from spreading throughout the state.

Figure 10 summarizes the spread of brook trout in lower Michigan. As late as 1882 none had been reported from the northeastern part of the peninsula--i.e., upper Manistee, Au Sable, Maple, Black, Sturgeon, and Pigeon rivers. Therefore, any decline of grayling in this region before approximately 1885 could not have been due to competition from brook trout.

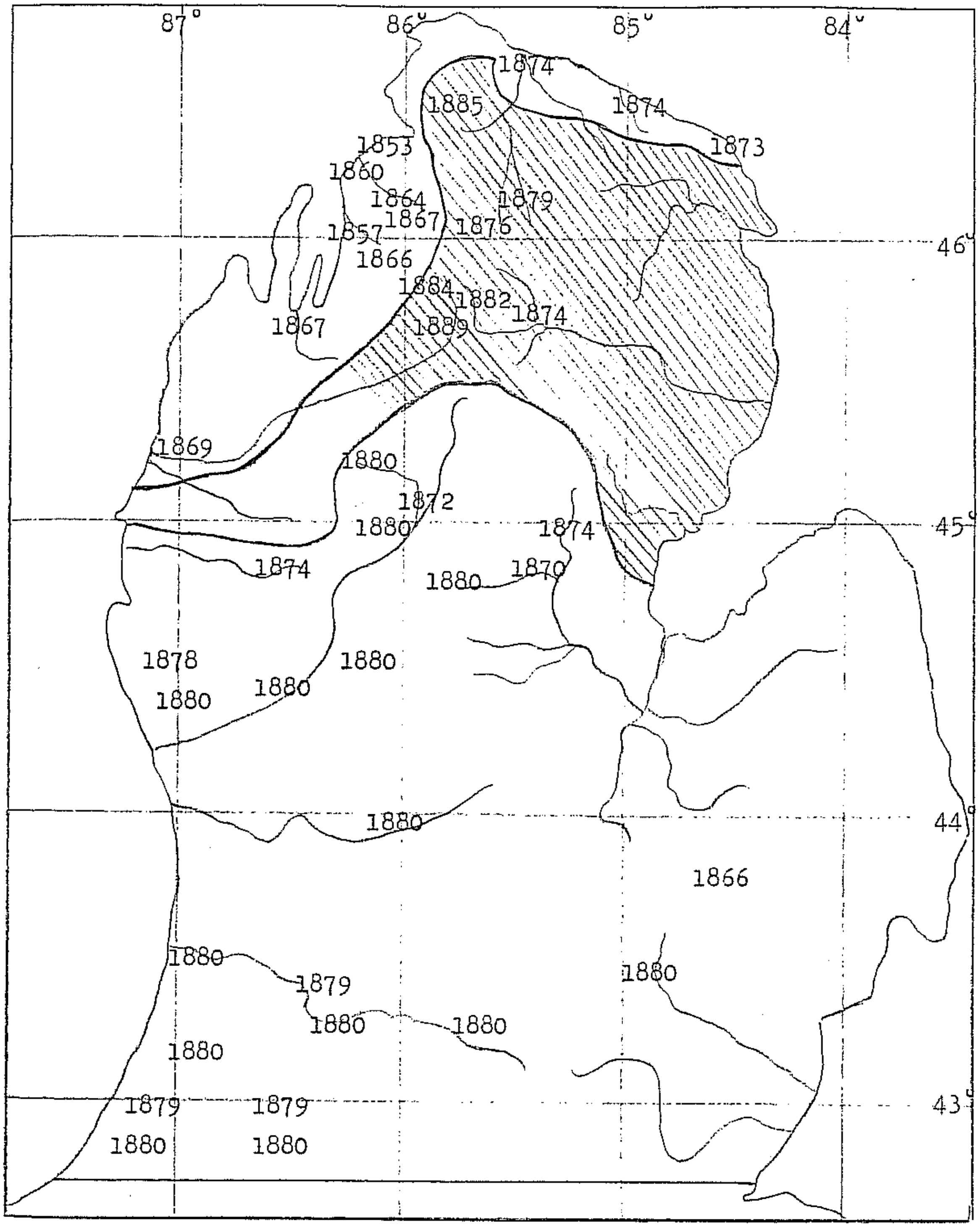

Figure 10.--Distribution and dispersal of brook trout in lower Michigan. The southern two-thirds of the state had no native brook trout; dates are the time and location of early introductions. The north and west sector is the natural distribution by about 1870. The central crosshatched section was the last area to be invaded by or stocked with brook trout; dates in the crosshatched section are when trout were reported as absent. Data from Table 9 and text.

TABLE 9.--Early introductions and records of brook trout in lower Michigan.

Date	Location	Authority
1866	Private ponds at Clarkston	Mershon, 1923
1870	South branch, Tobacco River	Mershon, 1923
1872	Caught 1 brook trout at Reed City	Metcalf, 1961
1874	Hersey Creek, Pere Marquette River, Tobacco River, and Upper Muskegon River	Mershon, 1923
1878	Oceana County	E.D.R., 1885
1879	Many brook trout have escaped from private ponds throughout state	Mich. State Fish. Comm., 1881
1879	Cass, Berrien, and Kalamazoo counties	Mich. State Fish. Comm., 1881
1880	Allegan, Berrien, Cass, Calhoun, Clare, Kalamazoo, Kent, Mecosta, Newaggo, Oceana, Osceola, Van Buren, Washtenaw, and Wexford counties	Mich. State Fish. Comm., 1881

The brook trout was probably not abundant in the upper Manistee River until after 1890 (Table 10). Although this trout was present in the lower river, it apparently did not move upstream but was established in the upper river by introductions. The decline of grayling was underway before brook trout was common (Figure 11). This curve, like the one of grayling decline in the Au Sable River, indicates that a factor other than competition was the major cause of decline.

As late as 1882 (Tables 13 and 14), reports were that the Au Sable River had no trouts. The grayling had been declining steadily for several years (Figure 12); by 1883 and 1884 there was considerable public pressure for the state to stock the Au Sable River with brook

TABLE 10.--Records of brook trout abundance in the upper Manistee River, Michigan.

Date	Observation	Authority
1875	No trout	Norman, 1887
1882	No trout	Norris, 1883
1884	No trout	Harris, 1884
1889	No trout	Herrick, 1926
1890	No trout	Hubbard, 1900
1900	Good trout fishing	Hubbard, 1900
1902	Good trout fishing	Harris, 1905
1904	Good brook trout fishing; no rainbow trout	Harris, 1905

trout. On page 33 of the Michigan State Board of Fish Commissioner's report for the years 1883 and 1884 was the following:

> For the past two years the Commissioners have been urged by several gentlemen whose knowledge of the river is full and accurate, to plant the famous grayling river, the Au Sable, with brook trout. They tell us the grayling is almost exterminated there. . . . We have very reluctantly come to the same conclusion.

This statement was a reversal of the decision made by the Commission in 1879 to the effect that grayling streams of Michigan should never be stocked with brook trout (Mich. State Fish. Comm., 1881). In 1885 the Michigan Fisheries Commission planted 20,000 brook trout fry in the Au Sable River. The location of this first introduction is uncertain. The Commission report (Mich. State Fish Comm., 1887) said the planting was in Grayling township; Mr. Peterson (unpublished notes)

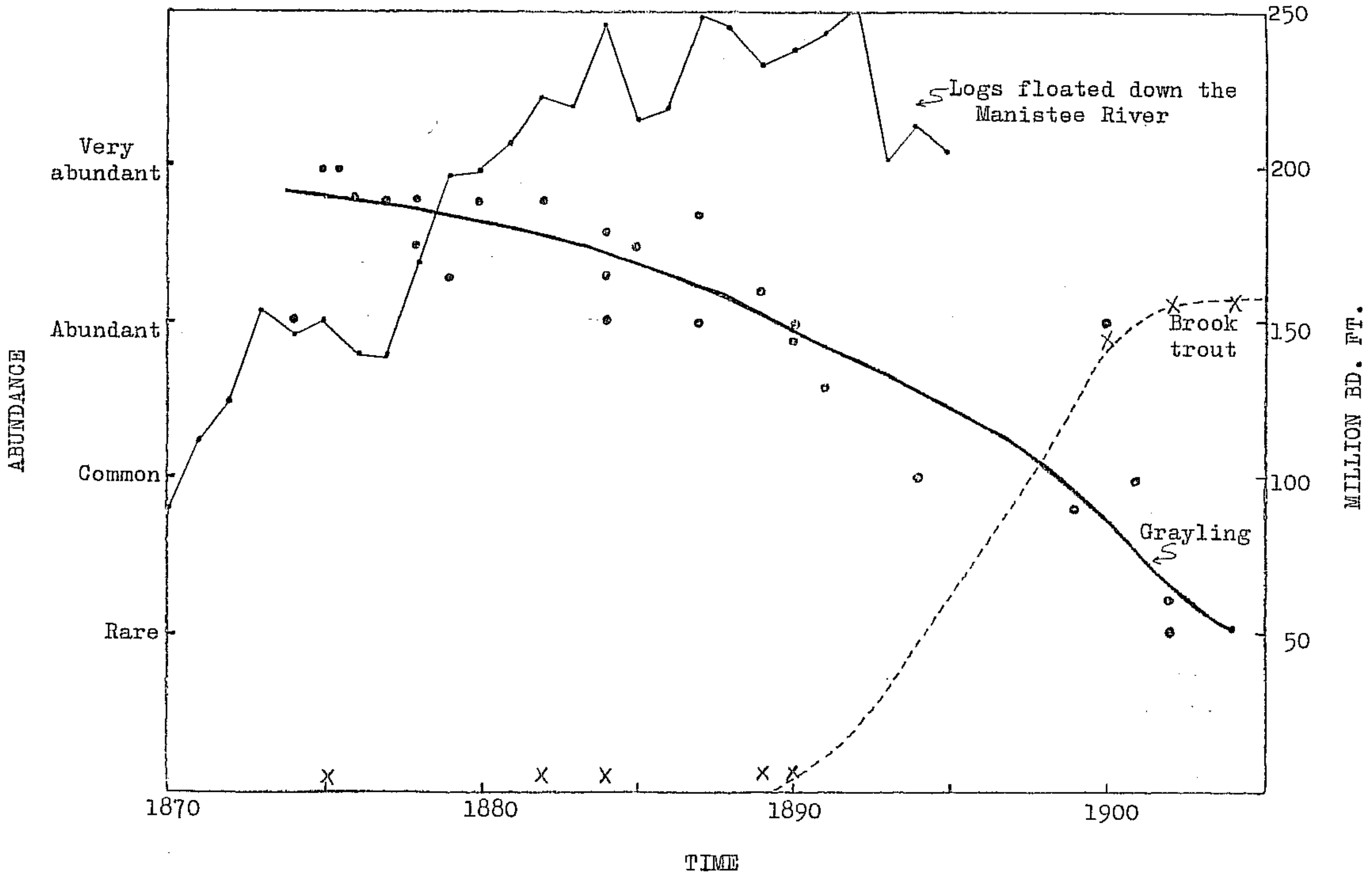

Figure 11.--The change of the game-fish fauna of the upper Manistee River, Michigan, from dominance by grayling to dominance by brook trout and the annual board feet of logs handled by the Manistee Boom Company. Data from Tables 10, 11, and 12.

TABLE 11.--Records of grayling abundance in the upper Manistee River, Michigan.

Date	Observation	Authority
1874	Abundant	Henshall, 1919
1875	Full of grayling	Norman, 1887
1875	Very abundant	Norris, 1879
1876	Excellent fishing	Hough, 1899
1877	Three men caught 600+ lbs. in two days	Furman, 1878
1878	Excellent fishing	Anonymous, 1880
1878	Three men caught 200 the first day	Nepigon, 1879
1879	Best fishing upper part, decreasing near Walton	Northrup, 1880
1880	Excellent fishing	Norris, 1883
1882	One man caught 212 in one day	Bower, 1882
1884	Caught lots	Anonymous, 1884a
1884	Caught 227 in two days	Harris, 1884
1884	Abundant	Mitchell, 1894
1885	Caught 200	Anonymous, 1885a
1887	300 fish taken	Mich. State Bd. Fish Comm., 1887
1887	Good grayling stream	Norman, 1887
1889	Lots	Herrick, 1926
1890	Fishing still good	Shields, 1892
1890	Caught 52 grayling in half a day	Hubbard, 1900
1891	Fair fishing	Macfie, 1895
1892	Upper Manistee, best grayling fishing in state	B. B., 1892
1894	Common in upper Manistee, rare elsewhere	Mitchell, 1894
1899	A few good catches in upper Manistee River	Harris, 1905
1900	Good fishing	Hubbard, 1900
1901	Three caught 100	Henshall, 1902
1902	Fished 100 miles of Manistee, only two	Harris, 1905
1902	Still some	Herrick, 1926
1904	Very few	Harris, 1905

TABLE 12.--Logs handled by the Manistee Boom Company at the mouth of the Manistee River, Michigan. From Hotchkiss, 1898.

Date	Board feet	Date	Board feet
1869	96,291,417	1884	248,812,668
1870	91,334,696	1885	215,641,134
1871	113,125,125	1886	219,384,703
1872	125,356,904	1887	249,956,859
1873	154,679,382	1888	246,090,313
1874	148,205,060	1889	233,146,927
1875	151,950,668	1890	238,128,770
1876	140,294,794	1891	242,336,590
1877	139,570,765	1892	252,801,657
1878	171,422,539	1893	202,203,183
1879	197,010,969	1894	214,226,973
1880	198,915,742	1895	204,195,371
1881	208,391,088	1896	223,688,575*
1882	223,844,838	1897	238,358,575*
1883	218,715,568		

*Also includes logs carried by railroad.

said, near Frederic; whereas Cooper (1952b) reported that brook trout was first introduced in the North Branch the same year.

Other fishes were planted in the Au Sable River before brook trout. In 1874 and in 1876 California salmon was unsuccessfully introduced (Mich. State Fish. Comm., 1876). The rainbow trout was first introduced in 1875 and a second planting made in 1880, but it was slow in becoming established (Figure 12). The first available record of catching trout in the Au Sable River was in 1884 (Anonymous, 1884d) when six were caught in a small brook a mile from the village

TABLE 13.--Records of rainbow trout abundance in the Au Sable River, Michigan.

Date	Observation	Authority
1867	No trout	Norris, 1879
1875	First planting	Bower, 1911
1876	First planting	Mershon, 1923
1880	Second planting	Bower, 1911
1882	No trout	Norris, 1883
1882	No trout	G. D., 1882
1884	Becoming a fine trout stream	Harris, 1884
1895	Estimated 25,000 removed	U.S. Fish. Comm., 1900
1897	Some	Anonymous, 1897b
1897	Caught 3 lb. rainbow	Harris, 1905
1898	Coming along good	Anonymous, 1898
1899	Caught 60 rainbows and brooks	Mershon, 1923
1910	One of best rainbow streams	Bower, 1911
1914	One of best rainbow streams	Smedley, 1938
1920	10 brown and rainbow trout caught for every brook trout	Irland, 1920

of Grayling. Mr. Hansen from Grayling (pers. interview) caught his first brook trout in this vicinity in 1887. The catching of a different fish caused considerable excitement among the local people.

In the Au Sable River grayling decline was advanced before exotic trouts could have been sufficiently abundant to be influential. When Figure 12 is compared with Figure 8 of the Jordan River, a marked

TABLE 14.—Records of brook trout abundance in the Au Sable River, Michigan.

Date	Observation	Authority
1867	No trout	Norris, 1879
1882	No trout	G. D., 1882
1882	No trout	Norris, 1883
1884	Caught 6 in a little brook 1 mile from Grayling	Anonymous, 1884d
1884	Becoming a fine trout stream	Harris, 1884
1885	20,000 fry planted	Mich. State Bd. Fish Comm., 1885
1893	5000 live were sent to Chicago World's Fair at 10¢ a piece	Irland, 1920
1895	U.S. Fish Commission took 8-10,000 spawners, estimated 75,000 brook trout removed from river this year	U.S. Comm., Fish and Fish., 1900
1897	Good trout fishing	Howe, 1897
1897	Abundant	Anonymous, 1897b
1898	A Detroit group took 1100	Hough, 1899
1899	Caught 400 in 2 days	Symes, 1899
1899	A Detroit group took 1800	Hough, 1899
1899	Caught 60 rainbows and brooks	Mershon, 1923
1902	Extremely plentiful	Henshall, 1902
1910	One of the best brook trout streams of Michigan	Bower, 1911

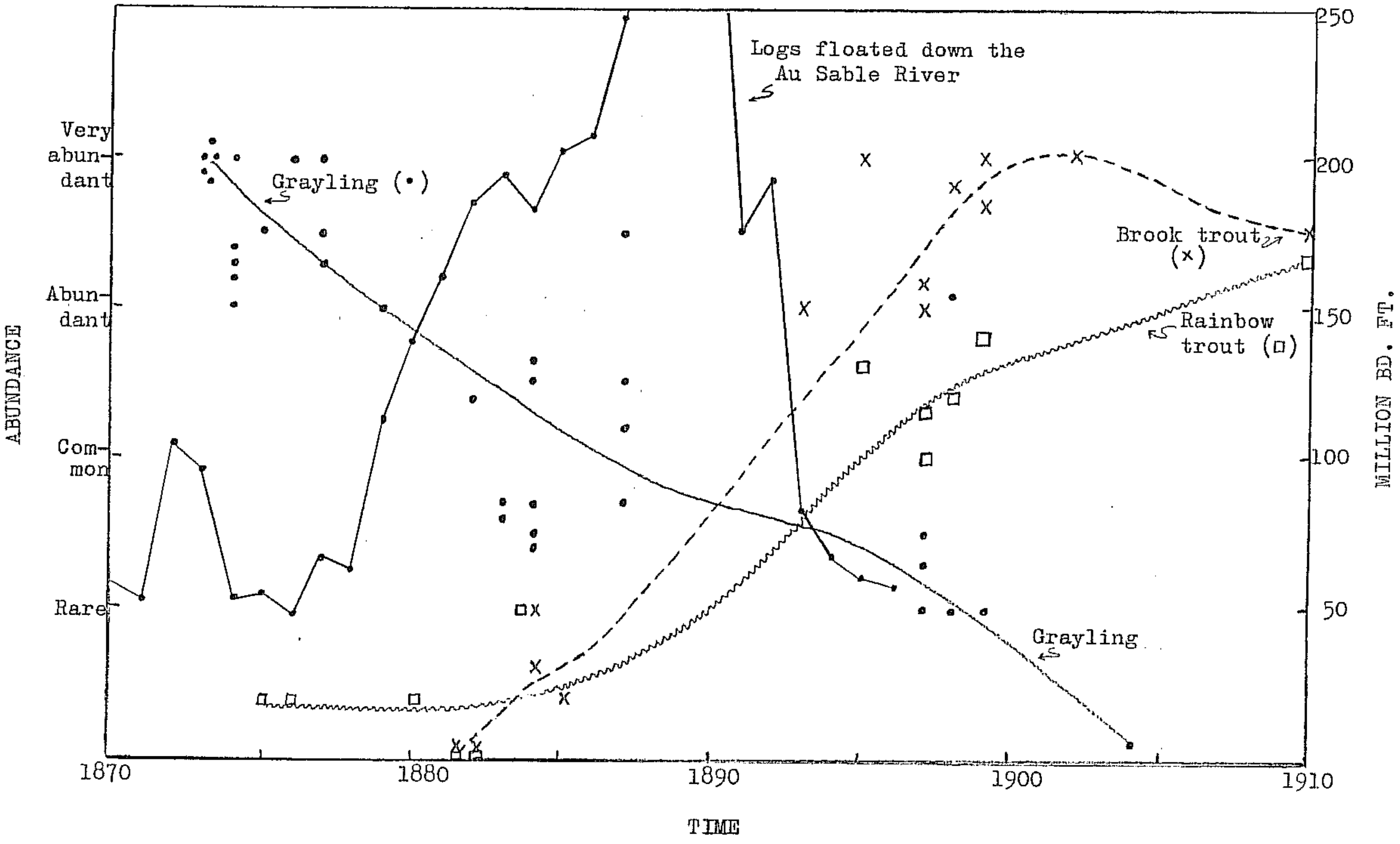

Figure 12.--The change of the game-fish fauna in the Au Sable River, Michigan, from dominance by grayling to dominance by trouts and the annual board feet of logs handled by the Au Sable and Oscoda Boom Company. Data from Tables 13, 14, 15, and 16.

TABLE 15.--Records of grayling abundance in the Au Sable River, Michigan.

Date	Observation	Authority
1873	220 fish in 2-3 miles	Fitzhugh, 1873
1873	Two men killed 2000 fish in a week	Irland, 1920
1873	Many large schools	Norris, 1883
1873	Caught 143 fish	Milner, 1873
1873	215 in 2 days by 2 men	Hallock, 1873a
1874	Abundant	Henshall, 1919
1874	Many	Norris, 1883
1874	Five casts, 15 grayling	Norris, 1879
1874	About 60 caught per person per day	Green, 1874
1874	Schools of 50 to several hundred	Mather, 1874
1875	Caught 118 fish in 2 days	Mather, 1875
1876	Packed on bottom like cobblestones	Banta, 1876
1877	Six people caught 285	Hallock, 1877
1877	5000 from 5 miles of stream	Norris, 1878
1877	Plentiful	Oatka, 1888
1879	Six people caught 950 in 5 days	Northrup, 1880
1882	Fished all afternoon to catch enough for dinner	G. D., 1882
1883	A few in lower reaches	Mich. State Bd. Fish Comm., 1885
1884	Occasional grayling	Oatka, 1888
1884	Becoming denuded of grayling	Harris, 1884
1884	Good fishing, 80 grayling per day	Anonymous, 1884a
1884	Good fishing	Anonymous, 1884b
1884	Some at mouth of South Branch	Goode, 1884
1887	Good grayling stream	Bissell, 1890
1887	Being depleted	Norman, 1887
1887	Poor fishing	Bebe, 1887
1887	Fished 3 days, caught 300	G. H. H., 1887
1887	Three people caught 330 in 7 days	Hasbrouck, 1887
1897	Light catches	Harris, 1905
1897	Scarcely any left	Anonymous, 1897b
1897	Very few grayling	Howe, 1897
1898	Almost gone	Anonymous, 1898
1899	Caught 60 trout and 1 grayling	Mershon, 1923
1904	Extinct	Harris, 1905

TABLE 16.--Logs handled by the Au Sable and Oscoda Boom Companies at the mouth of the Au Sable River, Michigan. From Otis (1948). (Data rounded to the nearest thousand)

Date	Board feet	Date	Board feet
1867	48,800	1882	185,400
1868	34,102	1883	194,600
1869	44,500	1884	176,038
1870	60,000	1885	201,438
1871	52,000	1886	207,458
1872	105,000	1887	249,173
1873	96,148	1888	283,782
1874	52,000	1889	294,975
1875	55,000	1890	324,504
1876	47,150	1891	175,332
1877	68,800	1892	192,088
1878	62,000	1893	83,546
1879	113,000	1894	68,885
1880	138,500	1895	60,239
1881	160,233	1896	57,530

difference is noticeable.

The Brook and Brown Trouts in Montana

Three species of trouts were introduced into grayling waters in Montana at nearly the same time. These, plus the indigenous cutthroat trout, were all possible competitors with grayling. That a major change in the fish fauna resulted is not surprising. As early as 1860, Head (1874) observed that cutthroat trout and grayling occupied the same streams. Other observers have noticed the compatibility of the two species (Brown, 1938a; Evermann, 1893).

Many grayling have been stocked in the waters of Montana since 1899. There is no way to evaluate the influence of these plantings upon existing communities. Some recent plantings of 6-inch grayling are doing well, but as a rule the early propagation of grayling fry probably had poor success.

Examples of coexistence

The grayling and exotic trouts are often, but not always, mutually exclusive. There are waters in which both have survived for a number of years. As was noted in certain Michigan streams and as is more pronounced in some Montana streams, a period of about 20 years coexistence is often common before a drastic grayling decline. To be a valid example, the two species should have been together longer than 20 years. Although it is not known when grayling or exotic trouts were first stocked in the grayling lakes in Utah, many have had brown, rainbow, or brook trouts for years. Miner and Mussingbrod Lakes, Beaverhead County, Montana, have also had brook trout and grayling for perhaps 30 years. It is true that generally whenever exotic trouts have been introduced grayling has tended to decline. Often a selective fishery and habitat change occur at the same time.

Grebe Lake. Grebe Lake at the headwaters of the Madison River in Yellowstone National Park is one of the few examples of a grayling population being superimposed upon a thriving rainbow and cutthroat trout population. Originally barren, the lake outlet was stocked with rainbow trout in 1889 (Jordan, 1891). In 1912 cutthroat trout was added (Kruse, 1959); by 1915 these two species were abundant (Kendall, 1915). Annual plantings of grayling began in 1921 (Kruse, 1959), and by 1930 all three species were doing well (Woodbury, 1930). In fact, Phillips (1926) said Grebe Lake was one of the best rainbow trout waters in Yellowstone Park. Since 1932 large numbers of grayling eggs have been taken from Grebe Lake spawning runs for artificial hatching. Some of the fry have been returned to the lake, but most have been planted throughout the West. In 1953 and 1954 grayling was 12 to 13 times as numerous as hybrid trout (Kruse, 1959). In this lake grayling was not introduced until after a trout population was established, and even with the drain on the population of removing spawn and a limited spawning area grayling has become the dominant species.

Elizabeth Lake. The grayling was introduced into Elizabeth Lake in the Belly River drainage of Glacier National Park in 1924. From 1920 to 1939 rainbow trout was also stocked. Both species have maintained themselves since the above dates. In 1959, 1960, and 1961 grayling made up approximately 40 per cent of the catch and rainbow trout, the remainder (pers. comm., W. M. Morton). From the one introduction grayling became established and successfully competed with rainbow trout for 37 years.

Upper Gibbon River. The brook trout and the grayling have existed together in the upper Gibbon River, Yellowstone National Park, between Gibbon Falls and Wolf Lake for many years. Although rainbow trout is common above and below this section, it avoids the intermediate area leaving mainly grayling and brook trout (Benson, *et al*., 1959).

Madison River

It may be well to separate the game-fish communities of the

Madison River into two geographical areas: the upper Madison River in Yellowstone National Park and the central Madison River in the vicinity of Meadow Lake. The brown trout appears to be the most important competitor, so it will be discussed most fully.

Upper Madison River. Habitat conditions appear to have changed little in the upper Madison since the early accounts in 1889 and 1891 by Jordan (1891) and Evermann (1893), respectively. Attention should then be focused upon fishing pressure, which was discussed in the previous chapter, and upon interspecific competition. Table 17 is a summary of the stocking, movement, and abundance of fish in the upper Madison River. The 1889 introductions placed the first exotic trout in the upper Missouri River drainage. The role of continued stocking of certain species upon their success in the community is unknown. In the 1930's and early 1940's grayling was stocked; more recently the emphasis has shifted to brown trout and rainbow trout. The occasional grayling now found in the upper Madison River probably drifted down from the upper Gibbon River.

Figure 7 shows the changes in the game-fish community and Figure 8 is a schematic presentation of this transition. The following sequence is suggested: natural fish community ⟶ introduction of exotics ⟶ build up of complex fish community ⟶ community including all species ⟶ sorting of community ⟶ decline or rise of certain species ⟶ new fish community of essentially new-species composition. The cutthroat and brook trouts survived in small turbulent tributaries, but the grayling, unable to tolerate such conditions, was nearly exterminated.

The introduced species required 20 years to build up a large

TABLE 17.--Records of game-fish abundance and introductions in the upper Madison River, Montana.

Date	Observation	Authority
1882	Grayling very abundant	Curtis, 1884
1889	Rainbow trout in Gibbon River	Jordan, 1891
1889	Brook trout in Firehole River*	Jordan, 1891
1889	Grayling very abundant	Jordan, 1891
1890	Brown trout in Nez Perce River	Jordan, 1891
1891	Grayling very plentiful	Evermann, 1893
1900	At Madison Junction there were in addition to native species: rainbow trout over falls from upper Gibbon River, brook trout from Firehole River, brown trout from Firehole River. Grayling, numerous	Fromm, 1941
1915	Madison recognized as a good grayling stream	Chittenden, 1915
1915	All native and all introduced species abundant	Kendall, 1915
1919	Brown trout has become dominant species	Mont. Fish and Game Comm., 1919
1921	All native and all introduced species abundant	Smith and Kendall, 1921
1925	Grayling appears to be holding its own	Russell, 1925
1926	Smaller tributaries, best brook trout streams	Philips, 1926
1926	Grayling locally abundant	Philips, 1926
1926	Brown trout, most abundant species	Philips, 1926
1933	Grayling greatly reduced	McCarty, 1933
1938	Grayling not very numerous	Back, 1938
1939	Brown trout, rainbow trout, few grayling	Simon, 1939
1953	Brown trout, rainbow trout, few grayling and brook trout	Benson *et al.*, 1959

*These were listed as brown trout by Jordan but must have been brook trout since the latter was abundant in the upper Firehole by 1891 and no record exists of its introduction.

population; then after a period of sorting grayling required about 20 years for decline. This same general chronology was followed by the game fishes in the Jordan River, Michigan, community (Figure 8). In contrast, in both the Manistee and Au Sable rivers in Michigan, the population increase of brook trout was nearly twice as rapid. The Jordan River is an example of competition and—as will be brought out later—the Manistee and Au Sable rivers, examples of habitat change. It appears that the upper Madison River community had the timing of a community disrupted by competition. There was an extended period during which all species were abundant, more so than some other rivers. Perhaps where no habitat change takes place the sorting of species requires a longer time.

Central Madison River. The central Madison River has undergone moderate habitat change, heavy fishing pressure, and community disruption by introductions like that of the upper river.

The brown trout reached the central Madison River from the Yellowstone Park introductions. No additional stocking of brown trout took place until approximately 1926 (Fuqua, 1929). The rainbow trout probably came from local introductions and downriver movement; by 1911 to 1916 both species were well established in Meadow Lake. This permitted about 20 years for downstream movement and establishment.

Records of grayling, rainbow, and brown trout abundance are in Tables 18, 19, and 20.

Figure 5 summarizes information regarding grayling, rainbow trout, and brown trout abundance in the Madison River. The grayling was plentiful until about 1920; by 1940 it was rare. The brown trout was first caught by local fishermen in Ennis Lake around 1910,

TABLE 18.--Records of grayling abundance in the central Madison River, Montana.

Date	Observation	Authority
1875	Poor fishing	Fromm, 1941
1880	Plentiful	Anonymous, 1920
1897	Many	Letter at Bozeman Fish Cultural Station, Henshall, Nov. 9, 1897
1898	Few	Anonymous, 1920
1899	None	Kohles
1903	Lots	Schbarber
1905	Best grayling fishing in the U.S.	Anonymous, 1920
1905	Buckets full	Baker, Sr.
1908	Boxes full (below dam)	Schbarber
1908	Pitch forked out of O'Dell Creek	Kohles
1912	Very abundant	Parker
1913	Par excellence grayling stream	Mont. Game and Fish Comm., 1914
1913	Catch many	Baker, Sr.
1913	Good fishing for grayling, O'Dell Creek	Mont. Game and Fish Comm., 1914
1913	Ennis Lake, fine grayling fishing	Mont. Game and Fish Comm., 1914
1915	Pitch forked out of O'Dell Creek	Kohles
1915	Buckets of grayling from O'Dell Creek	Baker, Sr.
1915	Big decline	Schbarber
1920	Trout most abundant	Anonymous, 1920
1921	Caught many grayling	Baker, Jr.
1929	Can catch out of any hole	Fuqua, 1929
1933	Completely gone	Baker, Jr.
1934	Some in Meadow Creek	Brown, 1938a
1936	Eggs taken at O'Dell fish trap	Brown, 1938b
1943	Rare, Ennis Lake	Brown, 1943
1951	Rare	Nelson, 1954
1954	Rare	Kruse, 1959

TABLE 19.--Records of rainbow trout abundance in the central Madison River, Montana.

Date	Observation	Authority
1913	Occasional	Baker, Sr.
1915	Good fishing	Anonymous, 1920
1920	Poor fishing	Anonymous, 1920
1920	Eggs from Meadow Creek	Anonymous, 1920
1923	Brown and rainbow trout dominant	Mont. Fish and Game Comm., 1923
1928	Big catches	Fuqua, 1929
1928	Very abundant in Meadow Creek	Fuqua, 1929
1934	Some in Meadow Creek	Brown, 1938a

and by 1913 to 1918 several accounts of brown trout abundance are recorded; it has continued as the dominant trout. Few observations on rainbow trout are available. But it appears to have reached a peak soon after brown trout (1920-1930), then declined.

Figure 5 suggests a relationship between the increase of brown and rainbow trouts and the decline of grayling. The general pattern is similar to that of the Jordan River, Michigan, and the upper Madison River, even including an approximate 20-year period for the rise of exotic trouts and another 20 years for the decline of grayling.

Meadow Creek, a tributary to Meadow Lake and a creek from which grayling spawn was taken for many years, had brown trout, rainbow trout, brook trout, and grayling as late as 1934 (Brown, 1938a). Again, the effect of artificial propagation is unknown, but Meadow Creek at this

TABLE 20.—Records of brown trout abundance in the central Madison River, Montana.

Date	Observation	Authority
1910	First large ones in Ennis Lake	Baker, Sr.
1913	Caught lots through ice	Baker, Sr.
1916	Lots	Schbarber
1918	Became thick	Kohles
1919	Lots	Baker, Sr.
1923	Brown and rainbow, dominant fishes	Mont. Fish and Game Comm., 1923
1923	9 million eggs from Madison Valley	Thompson, 1925
1924	12 million eggs from Madison Valley	Thompson, 1925
1928	Big catches	Fuqua, 1929
1928	Took 14 million eggs from Meadow Creek	Fuqua, 1929
1933	Peak of brown trout	Baker, Jr.
1934	Some in Meadow Creek	Brown, 1938a

time must have been in the sorting period when all species are present. This same period is evident in nearly every instance where competition may be a major factor. An introduced species must reach a certain population density in relation to the existing community and in relation to environmental resources before severe competition takes place (Crombie, 1947). In trout-grayling communities that have not undergone marked habitat change, it seems to require 15 to 20 years for the introduced trout to reach a severe competitive level, and then, a similar period of time for grayling decline.

Superimposed upon both of the Madison River fish communities has been increased fishing pressure during the period of competition. Grayling decline occurred at about the same time in both communities, although exotic trouts were present for a longer time in the upper river. Heavy exploitation, however, took place at the same time in the two communities.

Centennial Valley

In the Centennial Valley, Beaverhead County, Montana, Brower (1897) noted the abundance of cutthroat trout and grayling in the upper valley, and Henshall (Bozeman Fish Cultural Station, letter, Oct. 31, 1897) wrote that Upper Red Rock Lake was mainly a grayling lake. Blair (1897) advertised excellent grayling fishing in the streams from May to September. From 1898 to 1913 millions of grayling eggs were taken from Elk Springs Creek, which contained an enormous number of grayling (Henshall, 1907). Early settlers said that grayling continued to be abundant until approximately 1935 to 1940. However, Nelson (1954) found grayling rare in Lower Red Rock Lake and fairly common in the upper lake. This population is the only one within the original range of the southern populations that has maintained itself without extensive artificial propagation.

The rainbow trout was first planted in Culvers Pond in 1899 (Bozeman Fish Cultural Station planting records). Henshall (Bozeman Fish Cultural Station, letter, Feb. 10, 1903) commented on how successful the introductions had been. In fact, the Bozeman Station in 1905 received 40,000 rainbow trout eggs from this source. The species has continued to do well in Elk Springs Creek but elsewhere in the drainage is limited.

The date of the introduction of brook trout into the Centennial Valley is unknown. No mention is made of planting it in this area during the early years of the Bozeman Station when brook trout was planted throughout the state. Montana State put 35,000 brook trout in the Red Rock drainage in 1913 (Mont. Game and Fish Comm., 1914). This may have been one of the first introductions for local ranchers also mention this date as the approximate time when brook trout first appeared. The species has done well. Both brook trout and grayling were abundant for approximately 20 years before grayling began to decline. This again follows the 20-year cycle of the species in other streams where competition was important.

Local distribution of rainbow trout probably lessens its role as a grayling competitor. The brook trout, on the other hand, has spread throughout the valley, but it seems to have some separation from the grayling as the result of different habitat preference. The brook trout is mainly a permanent resident of the upper reaches of tributary streams, whereas grayling inhabits the lake and makes short spawning runs into the lower stream reaches.

Nelson (1954) found that grayling moved only a short distance up Red Rock Creek to spawn. It shows an inverse relationship to brook trout both in time and in distance upstream (Table 21). The question then arises, is this separation a result of competition, habitat preference, or both.

Section 1 is nearest the lake; the stream gradient is approximately 10 feet per mile; erosion is common; and the bottom is composed of fine gravel, silt, and sand. Section 2 has a gradient of 15 feet

TABLE 21.—Number of grayling and brook trout taken in three 600-foot sections of Red Rock Creek during the summer of 1952. Modified from Nelson (1954).

Date	Section 1		Section 2		Section 3	
	Grayling	Brook trout	Grayling	Brook trout	Grayling	Brook trout
June 28-July 1	9	1	7	10	1	50
Aug. 12-14	5	4	0	38	3	102
Sept. 12-14	0	1	1	11	0	56

per mile, and bottom materials are coarse and fine gravel. Section 3 is further upstream; the gradient is approximately 25 feet per mile; and the bottom materials are gravel and rubble. The grayling, then, is most abundant in sections 1 and 2, but the brook trout is more common in section 3. It is well established that brook trout do well in turbulent mountain streams but that grayling prefers a stream with a lower gradient and a non-rubble bottom. Since brook trout is relatively non-migratory in this area, beaver dams would not interfere with its life cycle as they do grayling.

Nelson (1954) found many more grayling than brook trout in Upper Red Rock Lake. The grayling, but not brook trout, spends much time in the lake. The few brook trout captured were taken near the mouth of Red Rock Creek. Therefore the main overlap in habitat is for a short period at the time the grayling spawn in the central section of the stream. However, since the concentration of grayling while in the stream is below this point and the concentration of brook trout is above, streams may not be an area of critical competition.

Discussion

The only clear example available of competition depleting a grayling population without other obvious factors is in the Jordan River, Michigan. Early decline was apparent before angling or habitat change were important. Several examples of coexistence have been mentioned: brook trout in Otter River, hybrid trout in Grebe Lake, and perhaps brook trout in Red Rock Creek. Some waters in which trouts and grayling coexist may be near the peak of the cycle when both species are common. The late arrival of exotics in some waters, i.e. Meadow Creek and Red Rock Creek, tends to put the cycle peak comparatively recently. Slight habitat change may slow down (upper Madison River) or increased change may accelerate (central Madison River) this competition cycle. W. G. E. (1897, p. 470) of Petoskey, Michigan, probably expressed the opinion prevailing at that time, "any angler knows that trout drive grayling from a stream, in time, but it takes a considerable number of years for them to do it. In the meantime there are both trout and grayling."

A difference in timing seems to exist between those waters where habitat change was important and those where competition was important. Where competition may be major, a 15-to 20-year rise of exotics and a 15-to 20-year decline of grayling is common. Usually those streams without competition have a short period when game fish are nearly absent; in contrast, those with competition have a period when all species are common.

When during the life cycle does competition take place? Food is often considered first in this regard. The adult grayling is not restrictive in food habits. Brown (1938a) found a great similarity between feeding habits of grayling, cutthroat, rainbow, brook, and brown trouts. The grayling and bluegills also feed on the same group of organisms (Leonard, 1940). Schumann (1958) concluded that both European and arctic graylings, in general, eat a cross section of invertebrate animals that occurs in the streams. Rawson (1950) and Ward (1951) agree that a grayling's diet is varied and that it depends upon the organisms available. Many introductions of yearling or older grayling have survived, but no reproduction resulted (Leonard, 1939; Lord, 1932; Mont. Game and Fish Comm., 1914; Tryon, 1947). Competition, therefore, must be most severe at some other point in the life history than for food of adults.

A second type of competition may be a predator-prey relationship. Both brown and brook trouts are fall spawners; thus, their young are feeding when the spring-spawning grayling is hatching. The first two or three weeks after hatching, grayling fry make little attempt to hide when disturbed (Nelson, 1954). Predation may be heavy at this time. Spring spawners, as cutthroat trout, do not have a size advantage over their own progeny or perhaps grayling fry (Benson, 1960). From brook trout taken in an area where grayling spawn, Nelson (1952) found no evidence of predation in the stomach analysis of 49 brook trout captured by angling, and in 97 stomachs collected by electrofishing two contained eggs and 13 contained grayling fry (Nelson, 1954).

Competition for spawning space seems unlikely since grayling prefers substrates of smaller particle size and since grayling is a spring spawner, whereas its main competitors spawn in the fall.

The ability of adult grayling to survive when stocked suggests that space or an ecological niche for adults is not a problem.

Fish eating of spawning eggs is usually not limiting (Greeley, 1933; Shetter, 1961; Smith, 1947). Brown (1938a) and Kruse (1959) found a few eggs in grayling stomachs, but these were probably just drifting eggs from spawning.

Thus, if competition is a factor, it must take place after hatching and probably before the yearling stage. In addition to predation at this time, competition for food may be important for fry. The grayling fry is much smaller than trout fry and has a smaller yolk sack that is absorbed rapidly. Small grayling began ingesting food at one week of age instead of two or three weeks like most trouts (Brown and Buck, 1939). In a hatchery 90 per cent of the grayling fry had food in their stomachs by the seventh day (Brown, 1938a). The grayling, therefore, has a critical period during which it must have quantities of a proper food supply. Time after time Brown (1938a) observed the tiny fish attempting to eat adult Entomostraca but without success. Apparently the small mouth prevented taking this large an organism until the fifth week. Chironomid larvae and pupae are one of the smaller foods that grayling fry utilize heavily (Kruse, 1954; Mather, 1875; Norris, 1883; Svetovidov, 1936; Wojcik, 1955). Leonard (1938) found the diet of brook trout fry to be 90 per cent Chironomid larvae and pupae. He cites other records of 70 and 73 per cent Chironomids in brook trout fry diets.

Since grayling, because of its small yolk sack and small size, requires suitable food during a critical period, depletion of that food source by competitors can be important. If abundant Chironomid larvae are not available during this three- or four-week period, the grayling fry can neither eat other insects nor, because of its slow development, can it readily swim to a different feeding area.

Just when in the life cycle keenest competition prevails is unknown. Probably this varies from community to community as different factors become limiting for each species. In Europe grayling and trouts live together in many streams with little evidence of harmful competition. In fact, the grayling has spread throughout England and Scotland in streams inhabited by trouts (Schumann, 1958).

Populations, as the two disjunct grayling populations that have lived in isolation for a long period, have not evolved mechanisms of interspecific toleration with ecological equivalents (Newman, 1956). This same type of situation is seen in island faunas and floras that are susceptible to exotics.

There is little doubt that grayling is highly intolerant of trouts. One can point to many streams that had grayling until brook trout arrived. It should be considered that many of the smaller tributaries where grayling persisted the longest were not optimum grayling habitat but were streams into which grayling was forced by changing conditions in the valleys. At the same time small headwaters are often optimum brook trout habitat.

Andrewartha and Birch (1954, p. 24) stated that "it is the quantity of the limited resource which determines the density of a population, not the intensity of competition" and continued to point out that the explanation for population decrease should be sought in the resource that is in short supply.

CHANGES IN LAND USE AND AQUATIC HABITAT

Man as a dominant organism upon the earth has a history of using more and more earthly resources in order to meet his rapidly rising needs. In many regions fresh water is one of the most critical resources. However, often rivers and streams are greatly changed not only by use of water itself but also by land use on the watershed (Eschmeyer, 1955). Water courses form long, sinuous ecosystems that expose much flank area to possible influence from land-use activities. It is this boundary phenomenon that makes aquatic habitats so easily influenced by land use.

Logging and agriculture, along with their many ramifications, are the two land-use practices most influential upon grayling habitat. Logging prevailed in the Michigan grayling region almost to the exclusion of agriculture, whereas the opposite was true in Montana.

Land cultivation or grazing was limited and widely scattered in central Michigan during the period of grayling decline. Its possible influence is so slight that it will not be considered except for the Otter River.

Agriculture on Montana Watersheds

In Montana, where decline of the grayling occurred later than in Michigan and where grayling habitat was in regions of the best local farm land, agriculture was extremely important. Irrigation was probably the most potent phase of agriculture, but land and stream-side clearing and grazing were also important. Since it is difficult to separate the effects of various aspects of agriculture, it is necessary to discuss several individual Montana watersheds and analyze the salient features of each.

Sun River Watershed

Nearly all bottom land in the lower Sun River Valley, Cascade County, Montana, is irrigated; uplands and slopes are pastured. The early practice was to water crops in late June and early July and to irrigate hay fields in late August (Wilson, 1893). Private irrigation started in 1868. Almost every homesteader built a dam to divert water from the stream bed. Before 1900 nearly all small tributaries were used for irrigation because they could be dammed easily and diverted through ditches to the low-lying valley floor. At this time stream flows were good and relatively stable. According to early settlers, it was difficult to find a shallow place to ford the Sun River. Now, during late summer, the stream may dry to disconnected pools.

The Fort Shaw Irrigation Diversion made water available for 252 farm units in 1910 (Bureau of Reclamation, 1948). By 1912 all except 36 farms were occupied. Willow Creek Reservoir, completed in 1911, blocked one main tributary of the Sun River. Construction of Gibson and Diversion dams, along with a reservoir-canal complex, began in 1913, making water available in 1920 for the 50,000-acre Greensfield Division. As water was removed from the river by both private and public projects, temperature of low, summer-water flows must have become higher than formerly, and the silt load must have increased from returning irrigation water and erosion. As early as 1905, the ordinary summer flow of the Sun River was nearly all utilized (Reclamation Service, 1907). Subsequent irrigation water came from the storage of flood flows.

The grayling, mountain whitefish, and cutthroat trout were abundant in the Sun River until the early 1900's. Mr. Ford (pers. interview), who has lived along the river since 1883, reported that grayling was seen in large numbers in clear holes until about 1908. By about 1913 the grayling was nearly gone. The rainbow trout was planted first in 1913 (Mont. Game and Fish Comm., 1914), and local residents reported the earliest catches of it by 1915. The brook trout was also introduced about this time but has never done well in this area. Since the exotics did not become well established until after decline of the grayling, habitat changes must have been the major cause of decline.

It seems doubtful that high water temperatures alone could have been the determinant of grayling decline in the middle and lower reaches of the Sun River. This fish was reported to be concentrated in the upper reaches and tributaries during late summer, although some were caught in the summer months from cold spring holes all along the river. If this upstream movement during the summer were necessary, dams that stopped migrations would keep fish from ancestral spawning grounds and restrict them to a section of the river that had higher water temperatures. The first small private dams for irrigation were simple rock barriers located on sites most favorable to divert water from the stream bed. These barriers usually washed out each year during spring runoff. As less favorable sites were used and better construction materials became available, more sturdy and higher structures were built. Federal participation in irrigation development from 1906 to 1920 accelerated complete or nearly complete blockage of fish movement. Upstream movement by grayling in the Sun River may have been an adaptation to avoid poor water conditions similar to the adaptation of northern grayling that move into clearwater tributaries during the summer.

The grayling diminished in the Sun River about the same time that large areas of land were opened to cultivation by development of water diversion and storage structures. Whether a temperature threshold, a blocked spawning migration, or the accumulated loss of tributary habitat was the major factor is not clear. Probably all were important. Competition with trouts did not seem to be involved.

Sheep Creek Watershed

Sheep Creek, a tributary of Smith River in Meagher and Cascade counties, Montana, is an example of optimum grayling habitat lying in optimum local agricultural land. The central portion of the watershed widens abruptly into a small mountain valley approximately 5-miles long and 1-mile wide. Sheep Creek meanders through this low-gradient section between willow-lined stream banks. Numerous small tributaries converge toward the main stream in the valley. Both below and above this valley topography steepens.

Head (1874), Ludlow (1876), and Prisson (1898) found grayling, mountain whitefish, and cutthroat trout very common in Sheep Creek. Mr. Coburn (pers. interview), who lived at the mouth of Sheep Creek on Smith River from 1898 to 1913, said that these same fishes, plus suckers, were abundant in that area. Around 1900-1910 Mr. Ford frequently fished the central section of Sheep Creek and caught many of the grayling. By 1915 a marked decline was obvious.

Five thousand each of brook and rainbow trouts were planted in Meagher County in 1898 (Bozeman Fish Cultural Station stocking records). Although the exact stream or streams involved are unknown, at least some of them could have been in the Smith River drainage. However, early settlers say that exotic trouts were not abundant until 1920. In 1915 a strange silvery "trout" (probably one of the introduced species) caught in Smith River caused considerable excitement because no one knew what kind of fish it was. The most abrupt decline of grayling took place before exotics were plentiful.

The only cultivation in the Sheep Creek drainage is in the lowlands of the valley where water rights were first taken in 1875, and all easily usable water had been commandeered before 1900 (Mont. State Eng. Office, 1950). Small springs and tributaries in the valley were diverted into ditches. The main stream was completely dammed in several places causing the channel to be dry in some sections until seepage re-entered the channel. Prisson (1898) mentioned that Sheep Creek runs through a section of mountain meadows where the slowly flowing water provides the best grayling fishing. This rich alluvial bottom land was the first and only area in the Sheep Creek drainage to be cultivated. It is the same area that has the necessary topographic features for grayling habitat.

Gallatin Valley

The Gallatin Valley, Gallatin County, Montana, including both the lower Gallatin River and the East Gallatin River with their tributaries, was probably at one time excellent grayling habitat.

The grayling was reported in the Gallatin River by Cope, 1872; Curtis, 1884; Evermann, 1893; Harris, 1887; Henshall, 1902; Jordan, 1891; Jordan and Evermann, 1902; and Milner, 1873. Nearly all the above authors found grayling coexisting with cutthroat trout and mountain whitefish. Interviews with seven early settlers during the summer of 1961 provided additional information for the period from 1900 to 1920. The grayling was abundant up to approximately the mid-1890's. Harris (1887) wrote of excellent fishing for this fish near the mouth of the Gallatin River. Evermann (1893), a few years later in 1891 while searching for a suitable fish hatchery site on Bridger Creek, noticed that Bozeman Creek abounded with the species. Apparently these observations were made near the end of grayling abundance, for on June 30, 1899, Dr. Henshall wrote in the appendix to his annual report: "The native fish of Bridger Creek are cutthroat trout, whitefish and an *occasional* [italics mine] grayling." Jordan and Evermann (1902) said that there were few grayling left in the Gallatin River. Early settlers of the Gallatin Valley agree that by approximately 1900 grayling was almost gone from the lower river.

A fish cultural station of the U.S. Commission of Fish and Fisheries was constructed in 1896 at the entrance to Bridger Canyon four miles east of Bozeman. Under the capable direction of Dr. James A. Henshall, who arrived early in 1897, this hatchery carried out the first introductions of brook and rainbow trouts into the Gallatin Valley. From hatchery stocking records and letters, the following fry planting data were assembled:

1897	Brook trout and rainbow trout escaped from the hatchery into Bridger Creek
1897	Rainbow trout were accidentally stocked in Bozeman Creek when buggy wheel hit a large rock and a can of 500 fry jolted into the creek
1897	Rainbow trout, Mystic Lake--25,000
1897	Rainbow trout, Willow Creek near Poney--10,000
1898	Brook trout, tributary of Rock Creek--5,000
1899	Brook trout, near Bozeman
1899	Brown trout, pond near Bozeman
1900	Brook trout, near Bozeman
1900	Rainbow trout, Bridger Creek
1901	Brook trout, near Bozeman
1901	Rainbow trout, Bridger Creek

The foregoing introductions of brook and rainbow trouts took place during the latter part of the grayling decline (Figure 13). The decline was abrupt, which, as discussed in the preceding chapter, is not typical of a grayling population when subject to competition. As early as 1911 (Field and Stream, Mar., 1911, p. 1095) the Gallatin River was being advertised as an excellent stream for brook, brown, and rainbow trout fishing. The fact that introductions of these trouts were not made until 1897 and then only in the headwater tributaries of the East Gallatin River (Figure 14) raises questions as to how influential they were in grayling decline.

There are no records of exotic trouts being planted in the West Gallatin River before 1902. Fish from a private hatchery or from the East Gallatin River may have been transported to the main river before official stocking took place. (William Dilts of Orando,

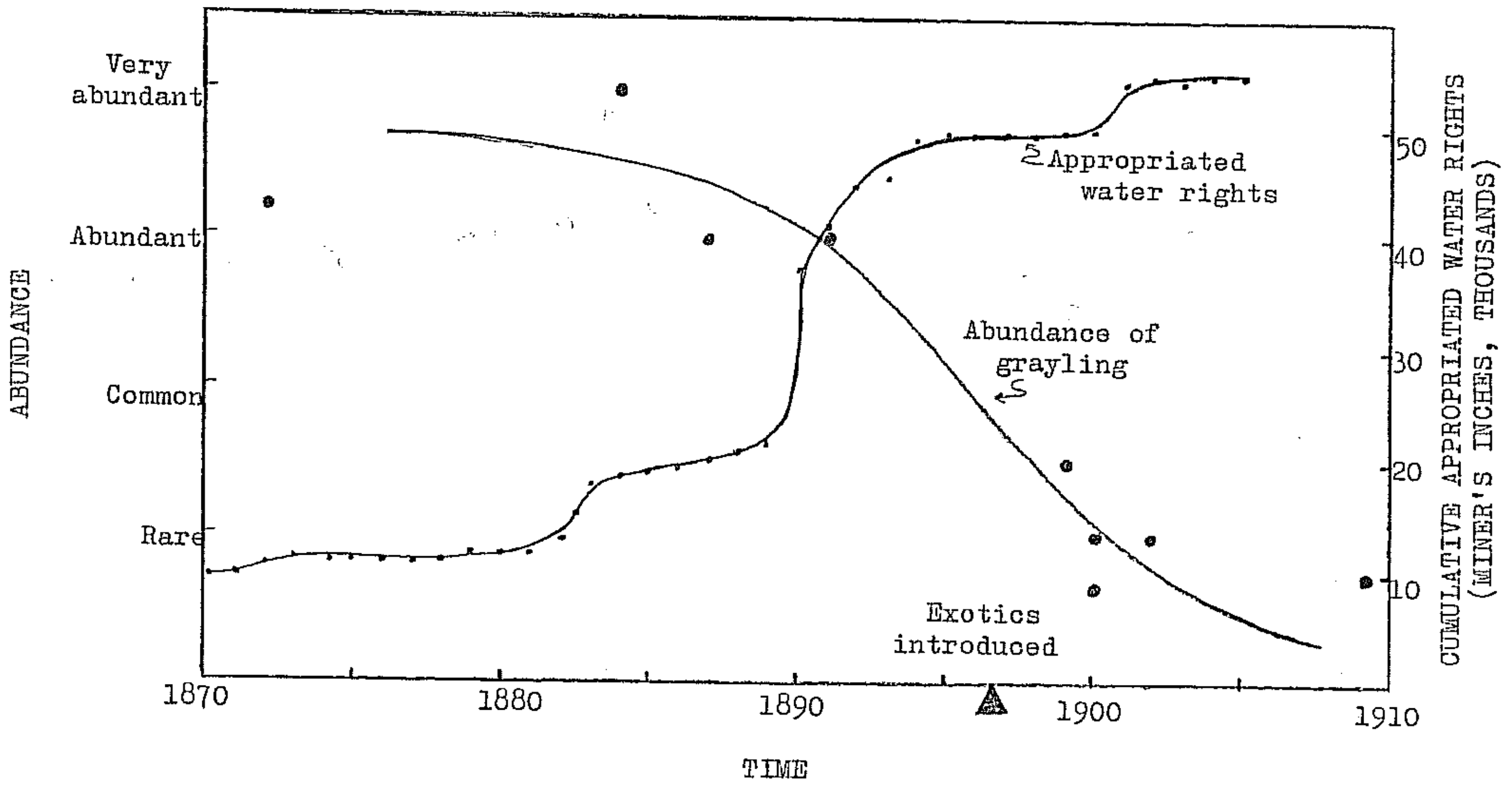

Figure 13.—The relationship of cumulative appropriated water rights and grayling decline in Gallatin Valley, Gallatin County, Montana.

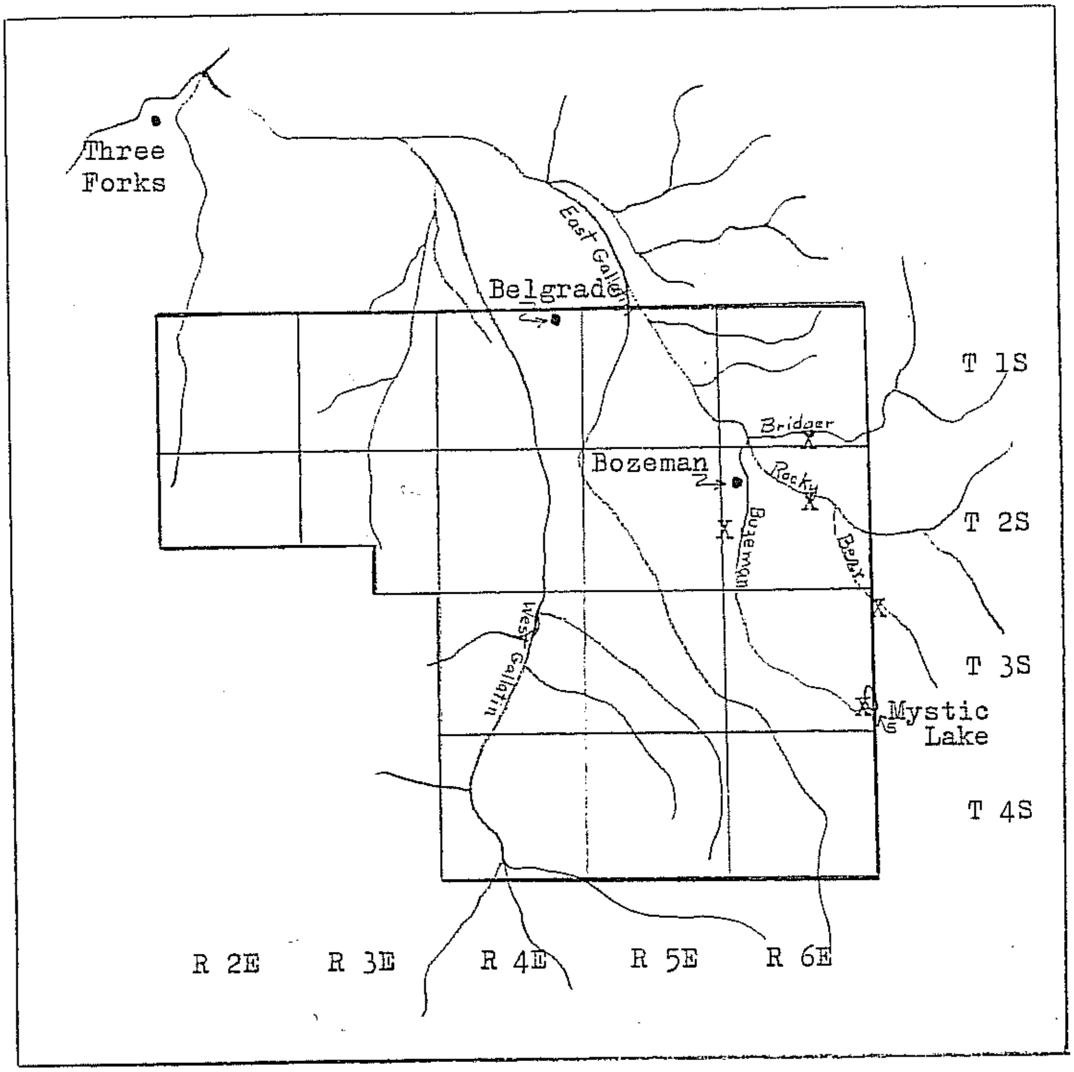

Figure 14.--Map of East Gallatin River and lower West Gallatin River drainages, Gallatin County, Montana. The approximate location of the first introductions of exotic trouts are marked by an X.

Montana, had a hatchery in 1897 from which trout, species unknown, could be purchased.) These early introductions did well, for in a letter dated July 7, 1899, Henshall said that brook and rainbow trouts, which had escaped two years before in Bridger Creek, were up to 12 inches in length. And in a letter dated November 9 of the same year, brook trout liberated in Bear Creek and Bear Gulch Creek in 1897 were up to 12 inches by that summer. (No mention was made in the stocking records of this plant. A Bear Creek tributary to Rock Creek is the probable location.) The rainbow trout of the same age in Mystic Lake was 10 inches, and in Bozeman Creek, up to 14 inches (Henshall, letter, Aug. 13, 1899). The rainbow trout did much better in Bridger Creek than brook trout (Henshall, letter, Mar. 20, 1900).

It was at the Bozeman Fish Cultural Station that grayling was first propagated in numbers. Beginning in 1898 eggs were taken from mature fish in Elk Springs Creek, and then in 1913, from Meadow Creek on the Madison River. Many of the early plantings up to 1907 were in the Gallatin Valley; after this, emphasis was on tributaries of Upper Red Rock Lake and on the Madison River drainage. There are few indications of success of these early attempts at artificial propagation.

A complex system of water diversion has greatly altered the natural drainage pattern of the lower river. In 1952, 107,261 acres were irrigated with about two-thirds of the water coming from the main Gallatin River (Figure 15). Hydrographs taken in late summer show a decrease in flow downstream (Hackett et al., 1960; see graph, p. 89). Some sections of the lower river are completely without water for short periods during August and September (Dunkel, 1955). In addition to the irrigated lands, approximately 150,000 acres of the watershed are dry farmed each year.

The first irrigation ditches were dug in 1864. A sharp increase in irrigated lands occurred in 1866 as gold miners flocked to the region. Before the turn of the century nearly all available water had been appropriated. In fact, on many tributaries a water right dated after 1880 is of little value since it receives only flood waters. First lands to be cultivated were those that lay favorably along the

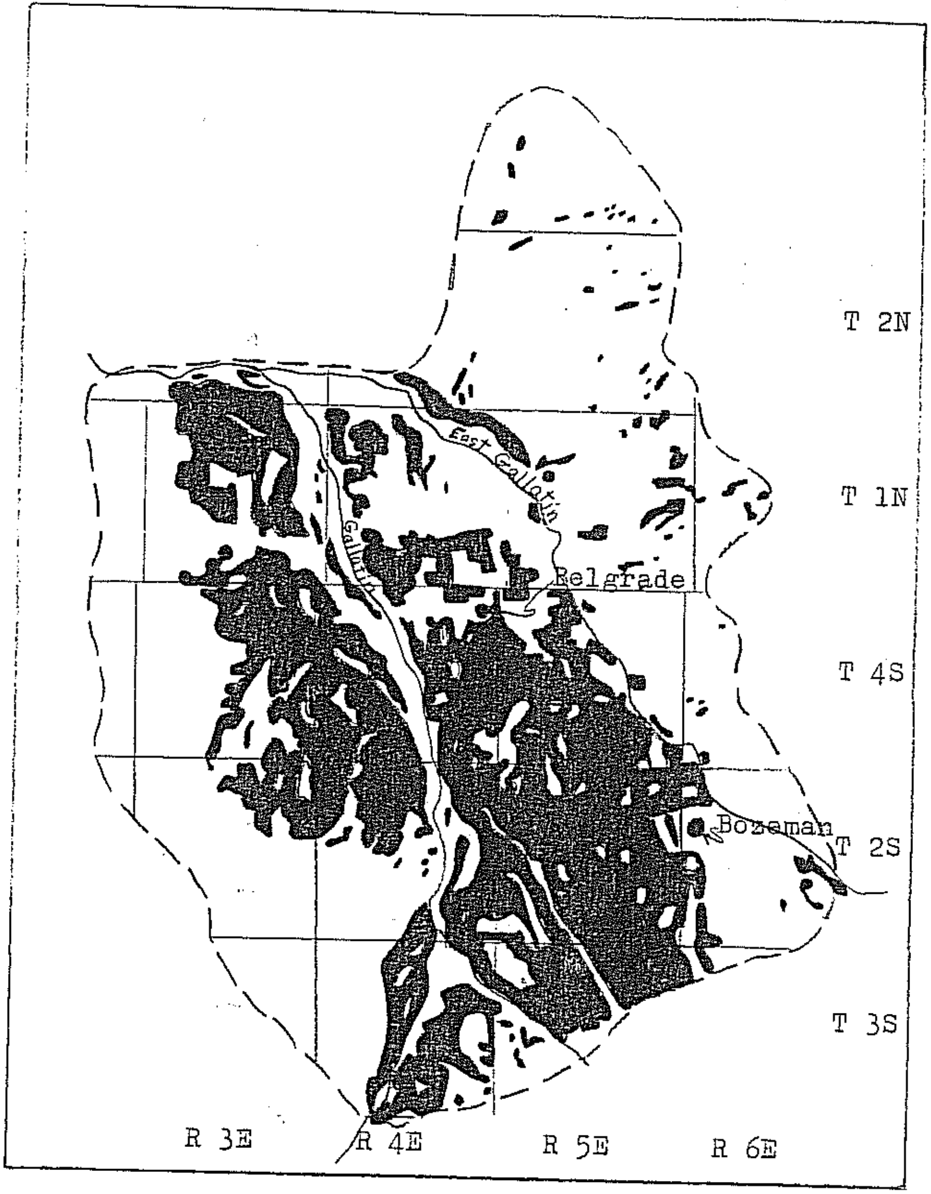

Figure 15. Map of Gallatin Valley, Gallatin County, Montana, showing the extent of irrigated lands in 1952. From Hackett et al. (1960, p. 36). Explanation: shaded areas are irrigated lands; dashed line shows valley border.

rivers and tributaries where small creeks and the main river could be developed easiest for irrigation. One of the larger diversions was completed in 1891: a 14-foot-wide canal from near the canyon mouth along the west side of the valley. In 1889-1891 a drought damaged many crops and caused the enlargement of irrigation systems (Newell, 1893).

Between approximately 1890 and 1900 the grayling population of the Gallatin Valley took a sharp drop and has never shown indications of recovering. Water removal from the streams began in 1865. After an initial rise, use was fairly constant until around 1882 when an increase began that rose abruptly in the late 1880's, culminated during the drought of 1890, then leveled off again after 1905. As an index of change in water use, the dates and amounts of water appropriations of the irrigation organizations listed in Water Resources Survey of Gallatin County (Mont. State Eng. Office, 1953) were tabulated as to total water appropriated for each year from 1865 to 1905 (Table 22). This is not a complete account of all water rights of the Gallatin Basin, but it provides an index of use increase. Figure 13 shows increase in use of water and, as far as data permit, decline of the grayling. The two lines have an inverse relationship. The requirements of grayling were once met in the Gallatin Valley below the canyon mouth. This was the same area in which irrigation became extensive, land was cleared, stream channels were changed, and small tributaries were diverted. Other fishes with less stringent ecological requirements than grayling could either survive under the modified conditions (as did the mountain whitefish) or else persist in the headwaters (as did the cutthroat trout) upstream from the agriculture zone.

TABLE 22.--Partial water appropriations from the Gallatin River drainage, Montana. Adapted from Water Resources Survey of Gallatin County, Montana State Engineer's Office, 1953. Amounts in miner's inches. (cfs = 40 miner's inches).

Year	Total	Accumulative total	Year	Total	Accumulative total
1864	200	200	1885	60	18,227
1865	1465	1665	1886	1600	19,827
1866	4283	5948	1887	1049	20,876
1867	255	6203	1888	1050	21,926
1868	1053	7256	1889	1785	23,711
1869	200	7456	1890	13,342	37,053
1870	2026	9482	1891	6601	43,654
1871	200	9682	1892	1820	45,474
1872	1125	10,807	1893	1147	46,621
1873	250	11,057	1894	2340	48,961
1874	328	11,385	1895	40	49,001
1875	175	11,560	1896	158	49,159
1876	0	11,560	1897	43	49,202
1877	100	11,660	1898	172	49,374
1878	125	11,785	1899	323	49,697
1879	75	11,860	1900	108	49,805
1880	100	11,960	1901	5000	54,805
1881	355	12,315	1902	79	54,884
1882	2074	14,389	1903	0	54,884
1883	3199	17,588	1904	373	55,257
1884	579	18,167	1905	51	55,308

The grayling remained longer in the lower Gallatin Canyon than in the valley area (Table 23). As mentioned previously, land and water use within the canyon has been and is limited, so habitat probably changed slowly. A limited area of suitable habitat enabled grayling to survive longer than in the intensely cultivated lower valley.

TABLE 23.--Comparison of grayling decline in the Gallatin Valley and in the Gallatin Canyon near Gateway, Montana. (Authorities without dates are from personal interviews in 1961)

Lower valley			Lower canyon		
Date	Observation	Authority	Date	Observation	Authority
1887	Abundant	Harris, 1887	1908-9	Abundant	Top
1891	Abundant	Evermann, 1893	1910	Occasional	Parker
1899	Occasional	Henshall, 1899	1914	Some	Allen
1900	Rare	Lane	1922	Few	Davis
1902	Very few	Jordan and Evermann, 1902			
1910	Occasional	Parker			
1913	None	Davis			

Madison River

Although the Madison and Gallatin are adjoining rivers, grayling decline followed a different pattern. In the Gallatin River decline was between 1890 and 1900; in the Madison River, Madison County, it was between 1915 and 1935. The decline was abrupt in the former, gradual in the latter.

Land and water use has been less severe in the Madison River drainage than in that of the Gallatin River. Irrigation above Meadow Lake in the Madison Valley is limited to scattered locations but becomes extensive in the Ennis area. The following data from Montana State Engineer's Office (1953 and 1954) illustrate some differences:

	Madison River	Gallatin River
Average flow	1,615 cfs	933 cfs
Maximum flow	7,750 cfs	7,870 cfs
Minimum flow	409 cfs	130 cfs
Drainage basin	2,485 sq. mi.	1,900 sq. mi.
Irrigated lands	7,984 acres	111,345 acres

The Madison is a larger river with a more uniform flow, partially because of two mainstream dams, and it has much less irrigated land than the Gallatin. Thus, habitat change was not as severe. Although irrigation is limited, it still may have been important to grayling by occurring on critical low-to-medium-gradient deltas and alluvial plains. Some changes did take place, for Thompson (1925) noted the changing water conditions and encouraged the stocking of brown trout since it was believed to be suited to the poorer waters. Populations of grayling remained high for nearly 20 years after cultivation became widespread. Under extensive habitat changes as occurred on the Gallatin River, a sudden population drop is expected, not a slow decline. The possibility must be considered that hatchery plantings of grayling supplemented the natural population in the Madison River.

What may happen under greater water use in the Madison Valley is suggested by the seemingly sudden decline in grayling just prior to 1900. Before the two reservoirs were formed, the large arable area near Ennis was deficient of water (Newell, 1893). The drought of 1890 to 1893 severely strained available water supplies. After construction of Ennis Dam and easing of the drought, grayling increased (Figure 5). The Ennis impoundment became suitable habitat for grayling to spend the non-spawning part of the year. The lake furthermore stablized water flows in the area and reduced demand on the tributaries for water.

In the Madison River both at Ennis and in Yellowstone National Park, the grayling and the introduced trouts were abundant at the same time. This did not happen in the Gallatin River drainage. There grayling was first abundant and subsequently it was replaced by introduced species. The Madison situation suggests competition, whereas the Gallatin, a habitat change that favored the new species.

In contrast to the Gallatin Valley, where accidental plants of trouts thrived and rapidly became dominant, the few plantings in the Madison River drainage did not seem to flourish. This suggests that the small introductions could not successfully compete with established populations. It took the well-established exotic trout populations of the upper Madison River to infiltrate slowly the natural population. This would be the more common occurrence unless, as in the Gallatin Valley, a habitat change favored the new species.

Centennial Valley

To appreciate habitat changes in the Centennial Valley, Beaverhead County, caused by man and by geologic aging, a more complete description of the watershed and a brief history of land use are necessary.

The Centennial Valley, approximately 50 miles long and 8 miles wide, is located just north of the continental divide in the southwestern corner of Montana. The southern slopes and valley floor are open meadows and sagebrush flats, whereas northern slopes are forested with spruce and fir. Water courses are commonly bordered by willows. This basin is the headwaters of the Beaverhead Fork of the Jefferson River.

Two lakes, Lower Red Rock Lake and Upper Red Rock Lake, lie in shallow depressions on the fairly level floor of the valley. Lower Red Rock Lake has approximately 1,126 surface acres and a maximum depth of 3 feet; Upper Red Rock Lake has 2,206 surface acres and a maximum depth of 6 feet, although much of the lake is less than 4 feet. A smaller lake, Swan Lake, with 323 surface acres, is connected to the upper lake on the north. Swan Lake has a water depth of 6 to 10 inches; high water temperatures are the rule from middle to late summer. Elk Springs Creek flows through Swan Lake and into Upper Red Rock Lake. All of the lakes are so densely vegetated that an airboat is required to travel on them.

Streams on the valley floor meander and are of medium gradient. Red Rock Creek, the principal inlet of Upper Red Rock Lake, flows westerly through both lakes and down the valley for approximately 12 miles below the lower lake into Lima Reservoir. Stream channels have been altered by diversion for irrigation and by beaver dams. Some smaller streams are diverted as they reach the valley to flow along small ridges, thus, making diversion for irrigation easier. This practice discourages the formation of well-defined stream channels. Stream bed materials usually consist of coarse-to-fine gravel in the upper valley and sand and silt near the lakes and in the lower valley.

Upper Red Rock Lake was found by Nelson (1954) to be homothermous with a maximum temperature of 76° F. during the summer of 1952. Red

Rock Creek reached a maximum of 65° F. during the same period. Elk Springs and Culvers Springs, tributaries of Elk Springs Creek, have nearly constant temperatures of 58° F. and 41° F., respectively (Banko, 1960).

History. Prior to the arrival of the first settlers in 1876 to raise cattle, the Centennial Valley had long been used by the Banncock Indians as a hunting grounds. By 1889 several ranches were scattered throughout the valley utilizing the abundant grass (Brower, 1897). At this time, according to Brower, the lakes were waterfowl hunting grounds, and water was used extensively for irrigation. Land-use conditions were fairly stable for a period as nearly all the land was owned by a few early settlers and kept within the family. Abuse through overgrazing was much less than in many other areas of Montana during this time. Even as late as 1953 the Centennial Valley had changed less than other areas of the Beaverhead River drainage (Nelson, 1954).

Red Rock Lake Migratory Waterfowl Refuge was formed in 1935 to benefit the trumpeter swan. The refuge is 40,000 acres in area and includes the three lakes, surrounding marsh, and land. Irrigation and grazing continues on the refuge. In fact, Graham (1959, p. 4) wrote that "cattle as well as swan apparently have priority over grayling."

In recent years habitat deterioration in the valley has become worse. Overgrazing is pronounced and water diversion to the extent of nearly drying up the streams occurs. Much of the abuse is in the upper valley where grayling persists.

Early settlers agree that the lakes and streams have changed. There is less willow along stream banks; Red Rock Creek has less flow and fewer holes than formerly; water fluctuations are greater.

Water diversion into irrigation canals carries many fry into fields. Nelson (1954) found an average of 0.5 to 2.5 grayling fry per cubic foot of water in irrigation ditches in late June and early July. These fry are quite helpless in water currents.

Changes in water depths. In 1896 Brower (1897) made a few soundings in Lower and Upper Red Rock Lakes. Depths recorded in the lower lake were 2, 3, 4, and 6 feet; in the upper lake, 10, 15, 20, and 25 feet. This is considerably deeper than the 3- and 6-foot maximum depths respectively reported by Nelson in 1954. It is nearly impossible for the basins to have filled to this extent, but it must be recognized that the lakes are rapidly becoming some shallower. About 1900 the Wetmores operated a hunting lodge on the south shore of Upper Red Rock Lake and used a paddle wheel boat to carry sportsmen out on the lake. This is a sharp contrast to 1958 when Montana State fishery personnel could not even paddle a rubber life raft through the aquatic plant beds to cross the lake.

Shallow lakes in regions of low precipitation, as those in the Centennial Valley, are sensitive to fluctuations in precipitation. In 1890 sections of Red Rock River were nearly dry in the course of the summer (Newell, 1893). During the severe drought of 1930 to 1936, the Red Rock Lakes were lowered considerably. In 1930 Lower Red Rock Lake was almost one-half its usual size--ranchers were mowing hay on what had once been lake bottom and the remaining water was stagnant (James, 1930)--so a small dam was constructed at the outlet to raise the water level. Even then for a number of years water covered only a fraction of the original area. At times between 1933 and 1937 there was no flow over the dam (U.S. Geol. Surv., 1959).

In 1895 an attempt was made to dam Red Rock River at the lower end of the Centennial Valley. A summer flood washed out the dam that was to store water for irrigation (Brower, 1897). It was replaced by Lima Dam that formed a reservoir near this site in 1902; but it was washed out again in May, 1933. Repair was completed the next year. Not enough water has been available in recent years to fill the reservoir.

No long-term stream flow records have been taken above Lima Dam. The data from below the dam are typical of other streams in the region and show the effect of the 1930 drought on stream flow in Centennial Valley (Table 24).

TABLE 24.--Regulated flow of Red Rock River below Lima Reservoir, Beaverhead County, Montana. Note reduced discharge during drought years of 1931 to 1937 (U.S. Geol. Surv., 1959).

Year	Flow (cfs)	Year	Flow (cfs)	Year	Flow (cfs)
1910	---	1925	---	1940	106
1911	---	1926	149	1941	64.8
1912	176	1927	170	1942	95.1
1913	270	1928	134	1943	141
1914	232	1929	114	1944	133
1915	228	1930	116	1945	129
1916	206	1931	69.4	1946	164
1917	240	1932	86.2	1947	188
1918	---	1933	91.9	1948	141
1919	---	1934	---	1949	145
1920	---	1935	59.5	1950	149
1921	---	1936	---		
1922	---	1937	60.6		
1923	---	1938	105		
1924	---	1939	---		

Organic matter typically builds up quickly in shallow lakes when rooted aquatic plants grow over the entire bottom. Added to the vegetative deposition in the Red Rock Lakes has been silt from the inlet streams, especially from meandering Red Rock Creek. Some bends on the ten-foot-high creek banks are eroded back several feet each year. Refuge personnel straightened the channel in 1960 to help reduce erosion and subsequent filling of the lake.

Banko (1960, p. 72) stated that "the very fertile bottom of Upper Red Rock Lake supports an almost unbelievably abundant and luxuriant growth of aquatic plants" and listed the following species and the percentage of lake area covered by each:

Upper Red Rock Lake

Species	Percentage
Elodea _canadensis_ Michx.	41
Chara spp. L.	22
Bare	12
Potamogeton _foliosus_ Raf.	5
_P_. _pectinatus_ L.	4
Miscellaneous	16

Lower Red Rock Lake

Species	Percentage
Elodea _canadensis_ Michx.	39
Bare	19
Algae	12
Potamogeton _richardsoni_ (Benn.) Rybd.	9
Sagittaria _latifolia_ Willd.	5
_P_. _pectinatus_ L.	2
Miscellaneous	14

The bottom of the Red Rock Lakes is a mucky matter composed of decaying vegetation, other organic material, and mineral soil. Decomposition is slow and the accumulation of organic matter on the bottom is greater than the annual deposition from life in the lake would indicate (Banko, 1960).

Results of changes. Through the combination of geologic erosion, human-accelerated erosion, and water-level response to fluctuation in precipitation, the habitat afforded by Upper Red Rock Lake is changing rapidly. The lake is now marginal for grayling, brook trout, and cutthroat trout, and probably only through the many cool, well-aerated springs and inlets are these species now able to survive in it.

Lewis and Clark reported catching what were later thought to have been cutthroat trout, mountain whitefish, suckers, and grayling in the upper Beaverhead River above Dillon, Montana (Coues, 1893). Evermann (1893) found grayling, mountain whitefish, suckers, dace, sculpins, and one specimen of burbot at collecting stations near Dillon and near the village of Red Rock. The burbot was reported by local settlers to Evermann as being common in Red Rock Lake. Lewis and Clark in 1803 found trout abundant and grayling apparently scarce, whereas Evermann in 1891 found grayling abundant but no trout in the same area at approximately the same time of the year.

Although there are no early records of non-game fishes in the Centennial Valley, it would appear that since all species common to the upper Missouri River drainage were found in the upper Beaverhead River they would also be in the Centennial Valley. In contrast to this is the almost unanimous opinion of early settlers in the Centennial Valley that no suckers were present in the Red Rock Lakes until after Lima Dam washed out in 1933. The common belief is that a concentration of suckers below the dam then moved into the lakes. It is untenable to accept the premise that suckers had not previously found their way up the easily accessible water course from the upper Beaverhead River. But undoubtedly suckers were not as abundant in the early 1900's as after 1940. The chronology suggests that habitat change may have been a factor. The low waters during the drought plus the gradual shallowing of the lakes changed the waters from being more suitable for grayling to being more suitable for suckers. Suckers, hardier fishes, thrived in the shallow waters, muddy, weedy bottoms, higher temperatures, and lower dissolved oxygen content.

Local residents have made suckers the scapegoat of the decline of grayling. From the unanimity of opinion, it is apparent that this topic is discussed often. New residents tell almost word for word the same course of events as old residents.

During the extremely low waters of the mid-1930's, local ranchers noticed many individuals of the grayling to be stranded and dying by the hundreds in Red Rock River below the lower lake and in the lakes themselves; only those spring-fed streams flowing into the upper lake had enough flow to sustain adequately the fish. During the dry years irrigation water was in greater demand; individual dams were made higher and tighter, further reducing the already limited flow.

Elk Springs Creek no longer supports grayling but mainly rainbow trout and, sparingly, brook trout. This stream has changed little in historic times, aside from the two ponds in its headwaters. The question can be raised whether Swan Lake may be acting as a block between the stream and the main lake. Being so shallow, the water must get warm and the dissolved oxygen content low. This could stop either the upstream spawning migration or, more likely, the downstream return of adults and young later in the summer. Unsuccessful attempts to restock Elk Springs Creek suggest that, since the creek is apparently adequate grayling habitat, inaccessibility of the lake may be interrupting the life cycle.

The Red Rock Lakes are the only natural lakes directly accessible to fishes in the basin of the upper Missouri River. Therefore, this is the only grayling population within the native range of the grayling in Montana to have this lake-inhabiting, spawning-migration life cycle. Populations in other streams probably followed a similar pattern except that it was between a larger river and a tributary for spawning or it was within the river from pool to riffle. Before intensive land use there were approximately 48 streams flowing into the Centennial Valley. In 1951 only parts of five streams remained accessible to migrating fishes (Nelson, 1954). Irrigation and beaver dams have been the major factors in this reduction. The loss of spawning area has unquestionably been serious. The dividing and subdividing of channels and reduction of already low flows have reduced the quantity of spawning area. The quality of spawning area has probably also suffered as land use with its attendant siltation has increased. For example, turbidity made spawning observations difficult in lower Red Rock Creek in 1952 (Nelson, 1954). The result of deterioration of stream habitat has been that grayling must spend more and more time in the lake.

Increase in use of lake environment has aggravated the effects of the changing lake habitat. Low dissolved oxygen content during the winter forces grayling into the few deeper or spring areas of the upper lake. There it must compete with the hardier suckers for limited space and oxygen. The suckers thrive in shallow, warmer waters during the summer and can withstand lower dissolved oxygen content during the winter than grayling. With the several-foot-thick ice cover for six to seven months and decomposition of the abundant vegetation, dissolved oxygen must be at a premium during the winter. The change in species composition from trouts to suckers when silt and temperatures increase is not uncommon. On the Tobacco River, Michigan, a marginal trout stream, the change is abrupt where soil type and land use change (Spaulding _et al_., 1961).

The importance of the longnose sucker as a food competitor with trout and probably also grayling is not clear (Brown and Graham, 1954). In Alberta partial control of longnose suckers increased the populations of the mountain sucker, rainbow trout, and lake trout (Rawson and Elsey, 1950). Removal of rough fishes, including many suckers, from Russian River, California, increased trout reproduction (Pintler and Johnson, 1958). Sucker fry were found amongst weeds and in backwaters of Yellowstone Lake and tributaries (Brown and Graham, 1954); these are the same areas that fry of the grayling seek.

The grayling in the Red Rock Lakes is being subjected to the adverse conditions of its lake environment, of migration route obstructions, and of deteriorating stream conditions. The brook trout, on the other hand, remains a permanent resident in the upper reaches of streams where neither siltation nor water diversion are as severe; its reproduction is not delayed or stopped by obstructions; and wintertime dissolved oxygen is abundant.

The grayling has persisted within its native Montana range by utilizing Upper Red Rock Lake after stream conditions became untenable elsewhere. Now, as the result of geologic aging of the lake and increase siltation from land use, the upper lake is gradually becoming only marginal grayling habitat but good sucker habitat.

Agriculture on the Otter River, Michigan

The grayling population of the Otter River, Michigan, was reported by Kroll in the late 1880's (East, 1930) to extend along a 6-mile section of North Branch Otter River immediately above Bear Creek (Figure 16). In this area the river meanders through limited bottom land of sandy, humus soil and this was the best section of the river for the grayling. Lowe (1926) in 1925 found grayling 2 miles further up the west branch of the Otter River than in 1923 but not up North Branch Otter River above "Hanchettes" Bridge. In 1926 grayling was 1 1/2 miles further up stream than in 1925. It seems that as land along the North Branch was cultivated and the river changed, the grayling moved down toward the forks and up the west branch into an area previously unoccupied by the species. Since 1914 water has been increasingly diverted from the North Branch Otter River for irrigation (Mich. Dept. Cons., 1935). In 1925 Lowe (according to Taylor, 1954) mentioned the radically changed conditions of the Otter River, the increased silt, the increased number of sand beds, fluctuations of flow, and deforested stream banks.

Barriers to Fish Movement

Migratory tendencies of grayling seem to vary according to the available habitat and existing conditions. The Michigan grayling was thought by many early observers to be sedentary, with no spawning migrations (Bebe, 1887; Bissel, 1890; Norris, 1883; Parker, 1888). Metcalf (1961) mentioned limited spawning runs in Hersey Creek, Osceola

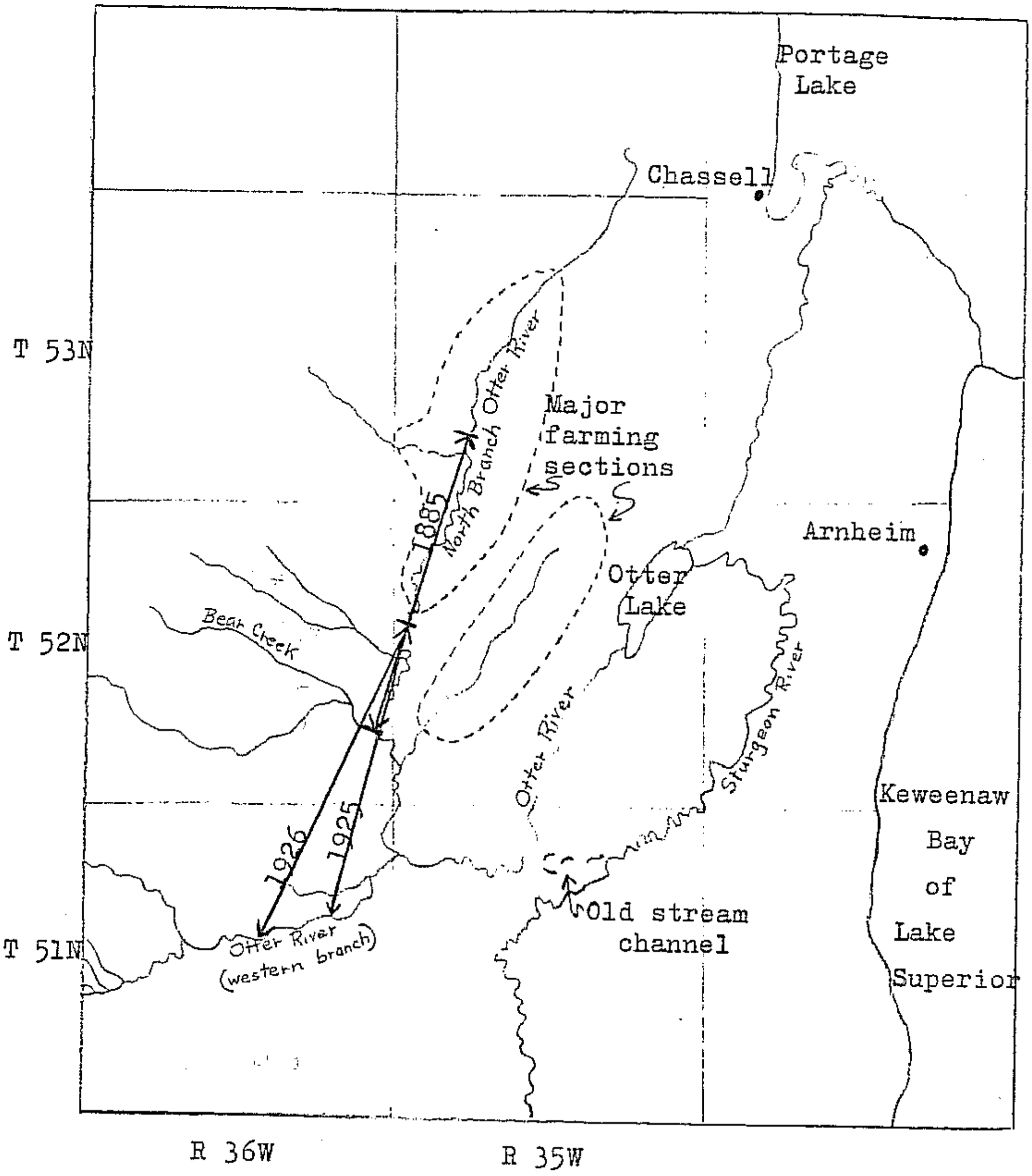

Figure 16.--The Otter River, Houghton County, Michigan. The section of river occupied by grayling has shifted away from the more extensively cultivated areas.

County, and Parker (1888) related the account of many members of the species being taken during the spawning season at the base of a recently constructed dam across the same creek. So at least in Hersey Creek, there was a seasonal upstream movement. Elsewhere in North America, the grayling may or may not migrate to a spawning area. Henshall (1907) reported, but did not document, long spawning migrations of nearly a hundred miles. Limited movements out of lakes into tributaries are the usual occurrence in Montana (Brown, 1938b; Tryon, 1947) and in Canada (Miller, 1947; Rawson, 1947c). In the Gulkana River, Alaska, the species moved only short distances, often only from pool to riffle for spawning (Schumann, 1958). Both Ward (1951) and Wojcik (1955) found that the fish in Canada and Alaska, respectively, usually moved up tributaries to spawn. Some individuals, however, may remain in the same stream all year. It is possible that with suitable year-around habitat, as Horsethief Springs or some of the Michigan streams, grayling did not migrate. In other areas where anchor ice, silting, limited food or space, high late-summer temperatures, and other such environmental factors may have become critical, migration was the rule. Therefore in many rivers any obstruction to free fish movement would be detrimental to grayling. Such obstructions could be in the form of large hydroelectric or water-storage dams, beaver dams, or semi-permanent water-diversion dams. The possibility of a thermal block in Swan Lake, Montana, was mentioned previously.

Beaver dams

Beaver dams in the Centennial Valley, Montana, were thought by Nelson (1954) to be one of the limiting factors for grayling. In

Alaskan streams (Wojcik, 1955) beaver dams concentrate grayling until periodic high water at least partially washes out the barriers. In small streams high grayling populations and high beaver populations could scarcely be compatible, especially in typical grayling streams, which are spring fed and have little fluctuation that could wash out such dams. Beaver were observed by Lewis and Clark (Coues, 1893) as being extremely abundant throughout the upper Missouri River drainage. In the Beaverhead Valley hundreds of beaver were seen basking in the sun, and slapping of tails at night interferred with men's sleep. During the era of the Rocky Mountain fur trapper (1820 to 1850), beaver were heavily trapped. This trend continued across the United States until the last of the 19th century when beaver were gone from many areas and conservation agencies started transplantation and other protective measures. Ranchers in the Centennial Valley, Montana, reported few or no beaver around 1900. In the mid-1930's beaver started appearing in numbers and dams were built on the tributaries to Upper Red Rock Lake. At this same time the newly established National Wildlife Refuge prohibited trapping of beaver about this lake and elsewhere on the Refuge. In 1936, 1944, and again in 1946, beaver dams across Red Rock Creek either stopped spawning migration or else trapped many grayling in meadows as they attempted to find their way around the dams. Large streams, such as the Beaverhead River and lower sections of Red Rock River, are large enough that spring runoff washes out many beaver dams each year. But the tributaries in the upper valley often do not have enough flow but what the dams may remain in place. Assuming that beaver were abundant in the Centennial Valley before extensive trapping, i.e., as found by Lewis and Clark in the Beaverhead Valley, how could grayling have utilized their present spawning areas? The available reports of great numbers of grayling coincide with the period of few beaver. Lewis and Clark apparently found no concentrations of grayling as were described later, for their keen observations and accurate notes would have surely recorded so striking a feature. Henshall (1907) has attributed to the grayling long spawning migrations from the Jefferson River to Elk Springs Creek. Could the grayling formerly have been restricted to larger rivers that could not be blocked by beaver dams? Could this be one of the reasons Lewis and Clark found so few grayling and why Evermann 90 years later in the same area found no trout and numerous grayling? Was the high grayling population observed in the Centennial Valley from 1870 to 1930 just a transitory population high during a man-caused low in the beaver population?

If indeed the grayling in Michigan was essentially non-migratory, it may have been influenced only little by the many beaver dams that must have been present before 1850. There are, however, no records of grayling abundance before 1850, so the population level is unknown. Migration did occur on Hersey Creek, and during the beaver era this stream must have had many beaver dams.

An illustration of possible fish access being blocked by beaver dams was found on the Brule River, a tributary of Lake Superior, in Wisconsin (O'Donnell, 1944). No mention of trouts in the Brule River was made by early explorers from 1680 to 1831. Accounts are written of gathering wild rice, hunting, and trapping, but not of fishing. Nearly all early journals expressed the difficulties of dragging boats over the many beaver dams. Michel Curot in 1803 and 1804 intensively trapped the watershed. First mention of fishes was made in 1831 by Schoolcraft. In fact, he commented that the river was filled with thousands of trout. But he made no mention of beaver dams although he traversed the area by boat. Later, in 1906, the migratory nature of the brook trout in the Brule River was mentioned. Could the brook trout in Lake Superior have been unable to move up the Brule River and establish themselves until beaver trapping reduced the number of beaver dams?

On relatively level land, where optimum grayling habitat is found, beaver dams are generally considered undesirable. Waters are warmed, fish movement is restricted, and spawning gravels are silted. Records do not go back far enough to indicate the level of grayling populations before beaver were heavily trapped. Our chronological view does not cover a complete cycle of grayling-beaver relationship. From current knowledge it seems best to deduce that high beaver and high grayling populations would have an inverse relationship.

It also could be speculated that beaver dams may have slowed the spread of brook trout in streams tributary to the Great Lakes. The brook trout was common in Lake Superior streams but uncommon and restricted in Lake Michigan and Lake Huron streams of the Lower Peninsula. As was discussed previously, the brook trout probably did not appear on the Lower Peninsula until after 1800. By this time beaver trapping would have made the small tributaries in which brook trout do so well more accessible than formerly.

Large dams

In Montana, Hebgen Dam, Ennis Dam, and Lima Dam would have stopped all upstream fish movement. Early settlers reported scooping up boxes of grayling at the base of Ennis Dam the year after it was completed. Apparently, Lima Dam also blocked grayling movement, for in 1911 a trip was taken to the dam to see if large numbers of fish were congregated below it as they had in previous years, but "practically none were seen" (Mont. State Fish Comm., 1912). Below a dam across Smith River many people gathered in 1899 to catch large numbers of grayling, mountain whitefish, and cutthroat trout that could not ascend the malfunctioning fish ladder (Anonymous, 1900).

A major effect of dams is that they have tended to drown the limited areas of grayling habitat. Hebgen Dam is a good example. One of the tributaries, Horsethief Springs, abounded with grayling (Evermann, 1893). The south fork of Madison River, which enters Hebgen Reservoir, also supported many grayling (Dwelly, 1892). Grayling Creek, which enters the reservoir from the north, was named after its plentiful inhabitants that covered the creek bottom (Anonymous, 1920). There were therefore at least sections of three important tributaries plus the main river that were destroyed as grayling habitat by a single dam.

Ennis Dam, Montana, was also constructed in an optimum grayling area. O'Dell, Jack, Meadow, and Cedar creeks all were reported to have large grayling populations and all are tributaries in the Ennis area. A good dam location for water storage requires a wide, low-gradient valley. These are the same topographic features that create grayling habitat.

The influence of reservoirs upon water temperatures of the Madison River are currently being investigated. Deep reservoirs, such as Hebgen, tend to lower downstream water temperatures, whereas shallow ones, such as Ennis, tend to raise the water temperature (Heaton, 1961).

The lentic environment of reservoirs favors new species that may compete with the established community. The Utah chub in Hebgen Reservoir is a good example (Graham, 1961).

Logging

Between 1840 and 1900 approximately 161 billion board feet of pine and 50 billion board feet of cedar, hemlock, and hardwoods were cut from the forests of Michigan (Maybee, 1960). Central Michigan was logged primarily between 1875 and 1895. As the timbered area and time of logging coincided with grayling distribution and the time of decline, many observers suggested logging as one of the main agents of the decline (Bissell, 1890; Bower, 1916; Harris, 1904; Mershon, 1923). Railroads were just beginning to reach the interior of the Lower Peninsula of Michigan, so rivers served as an excellent transportation system. Later, when logging railroads were common, many terminated at rivers, and logs were floated the remainder of the way to the sawmills.

Time of logging

An inverse relationship is suggested in the annual board feet of logs floated down the Manistee and Au Sable Rivers in relation to the time of grayling decline (Figures 11 and 12). These log data do not include all logs removed from the respective watersheds. As early as 1873 when railroads reached the pine regions, they also transported logs to milling centers. Rail log transportation followed the same general chronology as river-carried logs. The Michigan Central Railroad carried 50 million board feet of logs in 1873, the year it reached the village of Grayling. As the railroad extended northward and side roads were constructed, the annual board feet transported rose steadily; it reached 147 million in 1892 (Hotchkiss, 1898). On the west side of the Lower Peninsula, the Grand Rapids and Indiana Railroad carried 52 million board feet in 1874, 367 million in 1886, and declined to 95 million ten years later.

Most of the early logs transported by water were cut from the lower reaches of the watersheds; soon, as varied land ownership became common, scattered sections were cut along the water courses.

The middle and upper parts of the Manistee River basin were not extensively logged until approximately 1885 (Harris, 1884). A 16,000-acre tract of timber at the headwaters of the Manistee River was one of the last stands of white pine in lower Michigan. Owned by the Ward interests, this pine was cut between 1901 and 1912 (Leech, 1932). As late as 1903 the upper Manistee River flowed through many miles of uncut pine and hardwoods. This section of undisturbed habitat may have been a factor in delaying grayling decline in the upper river.

The first extensive logging on the upper Au Sable River was by A. A. Dwight in 1873. At this time he constructed a series of four dams on the North Branch creating 30 miles of slack water for log driving (Hotchkiss, 1898). On the main river the first timber camp was 20 miles below the village of Grayling in 1879 (Northrup, 1880). Much of the central Au Sable River country (vicinity of Mio) was logged in 1890 (Frothingham, 1905). Apparently, the region immediately below the village of Grayling was not extensively logged until around 1885. Decline of grayling prior to the logging of this region was probably the result of overfishing; neither introduction of trouts nor habitat changes due to logging had taken place. According to Mr. Hansen of Grayling (pers. interview), extensive numbers of logs were never floated down the upper Au Sable River for they were cut by the local mill.

Quid (1877) found no grayling in the North Branch of the Au Sable River until below Dam 4, the farthest downstream logging dam. From there to the main stream grayling was plentiful. Grayling access to the upper river may have been blocked by the dam, or perhaps the artificially created slack water was not suitable environment.

Fire

Fires started by lightning or by aborigines were probably a common occurrence long before white man entered the pine forest of Michigan. Forest cutting encouraged the growth of underbrush and left dead limbs and tree tops on the ground that were more inflammable than the original forests. Railroads, land clearing, transients, and logging operations started many fires. In 1880, 267 major forest fires were reported in Michigan; in 1881, one million acres burned; in 1894, hardly a county did not have a disastrous fire (Mitchell and Sayre, 1931). In 1908, 2,369,000 acres burned in Michigan (Pierce, 1909). Early settlers in Cheboygan County described the period from 1880 to 1920 as one of constant fires (Kilburn, 1960).

The effect of fire upon streams would be similar to intense forest removal whether by logging or by fire. Since forest removal had little obvious effect, fires also probably had little serious effect upon streams. Normally, only a limited area of a watershed would be burned during any one year; restoration of vegetative ground-cover is rapid in this region.

Influence upon streams

Decline of grayling and cutting of timber took place about the same time (Figures 11 and 12). The specific manner in which logging influenced aquatic habitat needs to be explored. There are two general aspects of logging that could seriously affect streams: forest removal and log driving.

Forest removal. Under different logging practices and on different soils, the removal of forest cover could instigate major changes in stream flow and water quality. Evapo-transpiration reduction from tree removal would not greatly affect stream flow in this region for water storage capacity within the root zone is low in sandy soils. Cutting practices at this time were to remove only the prime trees so that many smaller ones and a dense undergrowth usually remained (Spalding, 1899). Upland erosion would be nearly nonexistent because of the residual ground cover, low relief, and the sandy, porous soil. In the deforested and burned region of the upper Brule River in Wisconsin, which flows through a similar sandy soil, Evans (1945) found almost no surface runoff.

Because shading is one of the key controls over stream water temperatures (Greene, 1950), forest removal could have caused higher stream water temperatures. Stoeckler and Voskuil (1959) reported that shortening and diverting a spring channel through willows reduced the outflowing water temperature 10 to 11° F. Stream temperature may decrease as much as 12° F. after meandering through 400 feet of forest and brush cover (Greene, 1950). Lack of shade is one of the major causes of high temperatures in the Tobacco River, Michigan (Spaulding et al., 1961). Incipient high water temperatures could have been ameliorated in the grayling streams of Michigan by (1) water temperatures not being near the critical point before logging, (2) cool ground water (approximately 45° F.) continually feeding the rivers, (3) stream-side vegetation being secondary lumber species, i.e., cedar and hemlock instead of pine.

Generally, however, it seems that forest removal probably affected little the stream habitat of grayling in Michigan.

Log driving. Michigan streams were well suited for floating logs. They were swift but not white water; stream channels were well defined; flows were constant; and they extended into nearly all of the major pine region. Most cutting and hauling was done during the winter over snow and ice roads. Logs were then piled in the stream bed to await spring snow-melt and subsequent higher water flows. Water fluctuation on these streams was not great, even during spring runoff, so temporary dams were used to store water and flush logs downstream. Men were stationed at sharp bends and followed the logs to keep them moving. When the flow would no longer float the logs, another storage dam would suddenly be released to provide a flushing surge of water.

Before logs could be floated downstream, it was necessary to clear obstructions from both the channel and banks. Stumps and downed logs were removed or burned, brush was cleared, and shallow riffles were deepened (Hotchkiss, 1898). The debris, which had accumulated over the centuries and which effectively reduced bank erosion and stabilized the stream bed as well as provided fish cover, was removed.

The physical abrasion by logs during the drive was often great (Mershon, 1916), especially in shallow areas or in sections of stream meanders. As each wave of stored water passed, logs settled into the stream bottom until another surge arrived. In Sweden two major harmful effects of log driving (Malmgren, 1885) were damage to spawning beds and stream banks. U.S. Army Engineers concluded after a study of streams used for log drives in the upper Mississippi River-Lake Superior region that stream channels were completely disrupted and unstable. Channel configurations were changed. The artificial freshets had gradually widened the river beds and the cross sections became shallower (Rector, 1953). The once-stable stream beds now carried a heavy bed load of sand that filled holes, covered gravel bars, and filled the gravel interstices. Although this change came about quickly, the sands that became prevalent in the stream bed will require a long time to restabilize.

The bed of the Manistee River in 1884 was hard, yellow sand with occasional small clusters of rocks or organic matter and with scattered patches of aquatic plants (Harris, 1884).

In 1874 the bottom of the Au Sable River two miles below Grayling was clean sand and gravel in the center and a strip of dark humus loam along either side (Mather, 1874). Banks were lined predominantly by cedar, birch, alder, and willow. Many stumps, fallen trees, leaves, and weeds stabilized the stream banks (Mather, 1874; Northrup, 1880). Roots and litter from centuries of stream-side vegetation plus the absence of freshets had stabilized the easily erodible sandy stream banks; gradual sorting plus accumulated organic deposits had made a firm, stable stream bottom.

The repeated flushing by abnormal flows and gouging by logs quickly began eroding the unprotected sandy stream banks and the cleared stream bed. The stream had rarely been previously subjected to flood flows, and the banks and bed were not stabilized to withstand them. Hallock (1888) noticed that some stream bottoms were now of soft and yielding sand and that the sands were continually shifting.

The bottom material in the grayling streams of Michigan was in delicate balance with the water velocity. Various sizes of stream bottom particles have a safe water velocity below which erosion will not occur. For coarse sand the safe velocity is 1.5 to 2.0 feet per second. This velocity is only slightly less than that of many sections of the streams. Thus, a small change in any of the existing conditions may completely disrupt the equilibrium. Once sand is loosened and becomes water borne, stream bed erosion is accelerated. Moving sand functions as an abrasive, and when sand bars are deposited the water current is deflected against the opposite stream bank, beginning erosion anew. The same process occurs as stream gradient lessens when entering a lake, mountain valley, or backwater of a dam.

On the Tobacco River in Michigan, streambank erosion is the primary source of bed load (Spaulding et al., 1961). Erosion is more severe in the middle reaches than either above or below. This section combines moderate-current, meandering stream channel, and easily eroded soil. It is in the middle reaches of many rivers where grayling does best, but it is also this section that is most subject to erosion.

The slowness of stream bed stabilization after major disruption is shown by the Little Manistee River (Wicklund and Dean, 1957). This river was at one time a productive grayling stream and now supports a fair population of trouts. Water flow is stable, floods are rare. Eighty per cent of the drainage is optimum watershed. However, a high bed load of sand prevails in much of the stream, and shifting sand is the dominant bed type. The source of this sand is thought to be stream-bank erosion. Lack of escape cover and pools that resulted from erosion are limiting trout production.

It seems reasonable to hypothesize that before its use for floating logs the stream bed had stabilized to a great extent. Slow geologic erosion was, of course, taking place. The present condition is still the result of stream bed disruption because of log drives. Some stream sections are becoming stabilized, but others are still blanketed by large areas of shifting sand.

Susceptibility of grayling to habitat changes

Because of their particular habits, the grayling was vulnerable to the influences of log driving, especially when compared with exotic trouts that thrived under the changed conditions. Some of the major habits of grayling that contribute to this vulnerability are discussed here.

Place and time of spawning. As was discussed previously, the Michigan grayling was apparently quite sedentary, often spending all its life in one locality (Babbitt, 1900). However, other indications suggest—on some streams at least—a limited migration. They spawned in the main river and not in the small tributaries as brook trout (Bissell, 1890; Metcalf, 1961; Norris, 1879; Northrup, 1880).

The Michigan grayling spawned in April and early May (Bowles, 1874; Green, 1874; Hallock, 1877; Mather 1875; Milner, 1873; Norris, 1879); spawning seemed to be concentrated into a few days (Green, 1874; Norris, 1879). In northern Saskatchewan the spawning period is less than a week (Rawson, 1950); in Montana the spawning period is longer, but the main spawning run is often confined to two or three days (Brown, 1938b).

Nest construction. Spawning in Montana has been observed over sandy bottom (Tyron, 1947) and over 3 parts sand to 1 part gravel (Brown, 1938b). Grebe Lake inlet has a similar bottom composition. The section of Red Rock Creek used most for spawning was 33 per cent rubble, 31 per cent coarse gravel, 29 per cent fine gravel, and 7 per cent sand (Nelson, 1954). In the Otter River, Michigan, spawning gravels were about one-half the size of a pea to the size of a walnut (Taylor, 1954). Spawning took place over sand-gravel bottom in moving shallow water in the center of Michigan streams (Green, 1874; Mather, 1874). Green and Mather reported that Michigan grayling dug a redd (nest) and covered the eggs. Others have concluded, probably correctly, that grayling do not construct redds. No redds are formed nor are there attempts to cover eggs in Montana (Brown, 1938b; Laird, 1928) or in Saskatchewan (Ward, 1951). Advantage is made of natural depressions, or a slight depression is formed incidental to pre-spawning behavior.

Fabricius and Gustafson (1955) have reported on some careful observations of the spawning behavior of European grayling. The female by sharply bending the caudal peduncle and vibrating the tail and body would push the anal area into the substrate, often to the extent that the adipose fin was obscured from view. Eggs were ejected at this time. No attempt was made to cover the eggs, which rested in a small depression approximately 2 inches wide and 1 1/4 inches deep. Observations of this nature have not been made on American grayling, and the extent of similarity of behavior is unknown. Brown (1938b) observed ejected adhesive eggs being carried to the stream bottom by small sand and silt particles that stick them. This would require the presence of small particles on the stream bottom and a reduced current so they would not be washed away.

Egg characteristics. Egg production per female grayling is generally greater than that of competing trouts (compare Kruse, 1959, with Rounsefell, 1957). Egg size is smaller, approximately 3.6 to 3.7 mm diameter for water-hardened grayling eggs (Table 25) and 4.5 to 6.5 mm diameter for trout eggs (Rounsefell, 1957). Grayling egg diameter is about the same as whitefishes (Norden, 1961). The literature seems to be contradictory concerning egg adhesiveness (Table 26). Probably the time of observation accounts for the difference. The eggs are apparently adhesive immediately after spawning, but the stickiness is soon lost. The eggs are semi-buoyant (Schofield, 1928) and relatively lower in specific gravity than trout eggs (Henshall, 1899). They are thus susceptible to injury or displacement by an unstable stream bottom or fluctuations by water flow.

Spawning by grayling is commonly over a comparatively small particle substrate in areas of moderate current where a slight water velocity increase may be sufficient to move both bed load and the semi-buoyant eggs. Thus, once deposited, the eggs can be buried by shifting bottom and suffocate. Or, they may be exposed and swept away by the current.

It is now evident that log driving could have had a marked detrimental effect upon grayling. Log drives and artificial freshets

TABLE 25.--Summary of grayling egg diameter. Inches have been converted to mm.

Authority	Measurement
Water-hardened	
Smitt, 1895	4.0
U.S. Comm. of Fish and Fisheries, 1900	3.56
Henshall, 1919	3.6
Davis, 1953	3.8
Watling and Brown, 1955	3.76
Ward, 1951	3.53-3.78
Kruse, 1959	3.74-3.85
Not water-hardened	
Smitt, 1895	2.25-2.50
Rawson, 1951	2.54
Watling and Brown, 1955	2.40
Norden, 1961	2.5

were concentrated from April to June, the same period in which spawning occurred and fry hatched. Spawning was usually in the swift, shallow part of the stream where logs or flushing would tend to dislodge the eggs. Even if grayling had survived the initial period of log driving, the unstable stream bed was poor spawning substrate.

The introduced brook trout is a fall spawner and also frequently utilizes small tributaries and spring areas. There are indications that the spring-spawning rainbow trout did not do as well as brook trout when first introduced. The eggs of spring-spawning fish would be in the gravel during times of the moderate, natural spring freshets.

TABLE 26.--Adhesiveness of grayling eggs.

Authority	Location	Statement
Henshall, 1898b	Michigan	Nonadhesive before fertilization; adhesive after fertilization
Henshall, 1899	Montana	Nonadhesive
Brown, 1938a	Montana	Adhesive
Rawson, 1950	Saskatchewan	Nonadhesive
Davis, 1953	Montana	Adhesive
Wojcik, 1955	Alaska	Nonadhesive; adhesive when absorbing water
Fabricius and Gustafson, 1955	Sweden	Adhesive immediately after spawning but soon lost adhesiveness
Kruse, 1959	Montana	Adhesive; nonadhesive after water hardened
Baker (pers. comm.)	Montana	Adhesive

If the sandy bottom were likely to shift, it would do so during this time.

Fry development. The grayling fry has a long postlarval stage. Its small yolk sack is quickly absorbed and it must turn to ingesting food very soon (Brown and Buck, 1939), a characteristic similar to whitefishes. Therefore grayling fry must find quickly the proper food and a habitat niche. The fry is handicapped by being a fragile organism during this critical period and is unable to withstand or swim against much current. Grayling fry in Red Rock Creek, Montana, was relatively helpless in water currents for two to three weeks after hatching; many young of the species were carried downstream; others stayed in back waters and protected areas (Nelson, 1954). Average stream velocity was less than 1.8 feet per second. Harper (1948) noticed that small grayling fry in the Keewatin streams of Canada remained along the edge among rocks and vegetation in order to avoid the current. In hatchery troughs it is necessary to restrict water flow so newly hatched fry will not be washed against the tail screens (pers. comm., Harry Baker, Jr. and Hans Peterson). As early as three days after hatching, the grayling swims up and distributes itself throughout the water. It moves up from the substrate and must begin seeking food before it can maneuver in a current.

Clearing of rivers for log drives removes essential fish cover. Male grayling establish territories (Kruse, 1959) that are often bordered by debris in the stream. Fabricius and Gustafson (1955) felt that this was an important factor limiting European grayling in cleared Swedish rivers. Protected areas for fry are also greatly reduced; few eddies and backwaters remain. Vegetation along the shoreline is eliminated.

It seems doubtful that changes in food supply were important. Exotic trouts, whose diet is similar to grayling, flourished. The European grayling did well on the changed food supply of streams cleared for logging (Müller, 1954).

Absence of yearling grayling

The reproductive phase of a life cycle is nearly always the time during which a species is most vulnerable to adverse environmental conditions. This seemed to have been true of grayling. The few small fish taken during the latter years of grayling decline on the respective rivers were mentioned in many reports: Anonymous (1884a) on the Au Sable, Hallock (1875) on the Boyne, Hallock (1888) on the Little Manistee, G. H. H. (1887) on the Au Sable, Hubbard (1900) and Mershon (1923) on the Au Sable and the Manistee, and Norman (1887) on the Boyne in 1875 to 1876.

Discussion

There is evidence from several rivers that grayling decline was caused by changes in aquatic environment: changes associated with both farming and logging. Many aspects of agriculture may infringe upon rivers, but logging, as practiced in Michigan, disturbed rivers mainly through log drives.

In mountainous regions farm lands occupied the areas where the best grayling habitat was found. If irrigation were necessary, as in the upper Missouri River basin, there was direct competition for water.

An example of the indirect effect of cultivation upon a stream can be drawn from the investigations of Boussu (1954) and Holton (1953) on Trout Creek, a tributary to East Gallatin River, Montana. Their studies are not directly related to grayling but they do describe the creek. From the location and characteristics of the stream, it is easy to postulate that Trout Creek was formerly a grayling stream.

The 5- to 15-foot-wide creek meanders across a flat valley floor. Throughout its course a 3- to 8-foot-deep stream channel has eroded in the valley alluvial deposits. Water velocity is less than 2 feet per second as smooth-water riffles comprise approximately 40 per cent of the area. Aquatic plants are abundant in the 5 to 9 inches of water. Bottom deposits are silt, sand, and organic matter. Average maximum water temperature was 60° F. in 1951; maximum was 63° F. The stream remains ice free because of its springs origin. Under primeval conditions this was a cool, even-flowing, low-gradient, sandy, ice-free stream in which grayling would be expected to thrive. It now supports a limited population of brook and rainbow trouts.

Currently, nearly all the watershed is cultivated or pastured. The stability of the easily eorded stream banks has been upset by clearing, trampling, and flooding. On February 9 and March 26, 1951, floods caused severe eroding of the stream banks and scouring of the stream bottom.

The loss of small tributaries like Trout Creek was critical for the Montana grayling. Heaton (1960) concluded that loss of tributary habitat because of irrigation was limiting fish production in the Big Hole River drainage, Big Hole County, Montana. The rapid decline of grayling in the Gallatin Valley is an example of how vulnerable grayling were with this link absent. Sheep Creek, Montana, is a typical example of intense tributary use (Figure 17).

Droughts cause a greater demand upon an already abnormally low flow. The drought of 1890 to 1893 probably was the threshold for grayling in the Gallatin Valley; in the Centennial Valley the drought of the 1930's seems to be the turning point. Unusual climatic occurrences tend to aggravate existing critical relationships, e.g., suitable spawning and nursery area in the Gallatin Valley and competition with suckers in the Centennial Valley.

In Michigan because of the nature of the topography and soils, floating logs down the rivers seems to have played the major role in habitat deterioration. Forest removal and fire were of limited

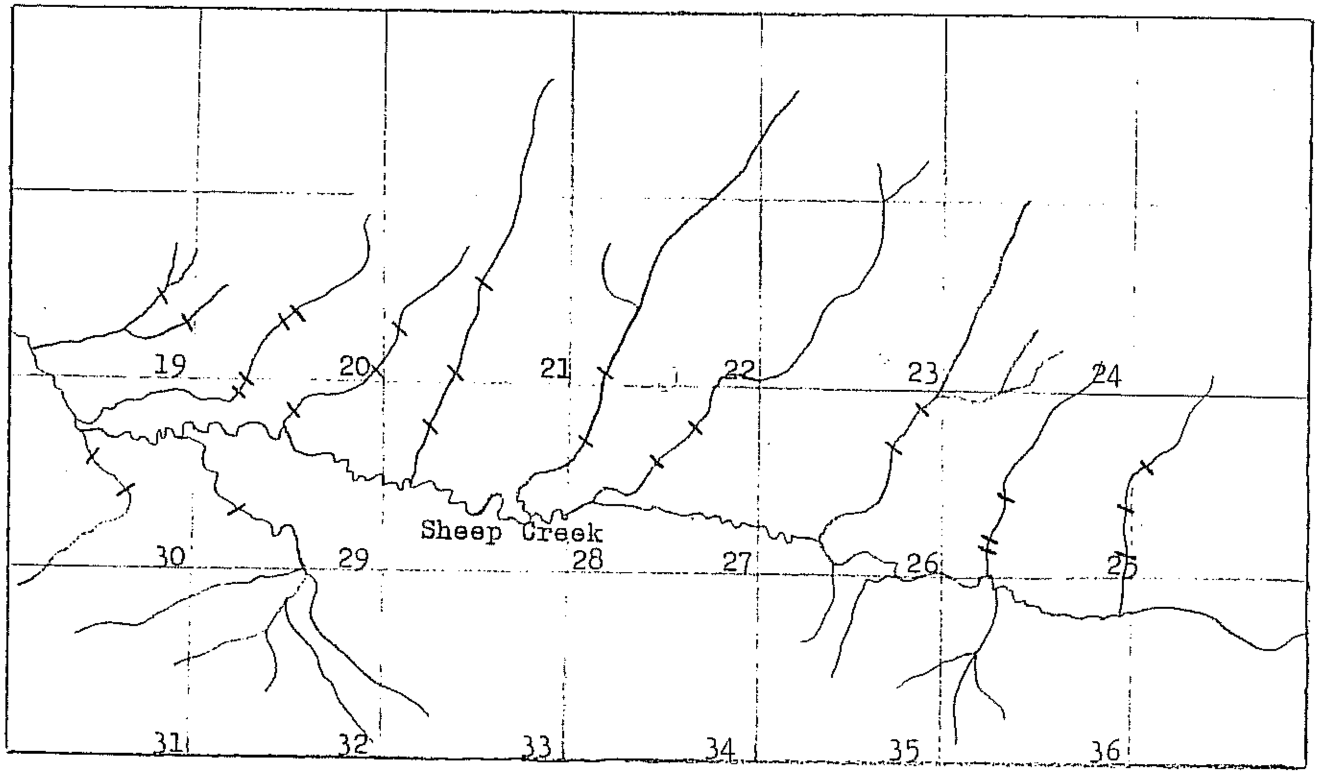

Figure 17.--Sheep Creek, T 12N, R 7E, and R 8E, Meagher County, Montana. This is the same stream section that at one time supported a high grayling population. Note the many irrigation diversion dams across tributary streams. From Mont. State Eng. Office, 1950.

importance. Disrupting the stream-bed stability caused heavy egg and fry mortality. This was probably the same life history stage that was most affected in many Montana streams by the drying up and changes in small tributary streams.

The grayling did well in Michigan because of the same environmental features that made the stream beds easily disturbed by log driving: uniform flow and sandy bottom. The stream bed was not stabilized sufficiently to withstand periodic artificial floods and abrasion from logs.

GENERAL DISCUSSION AND CONCLUSIONS

Matthiessen (1959) concluded that the great majority of animal species in danger of extinction had two characteristics in common: (1) they had a localized distribution before white man came, and (2) they were unadaptable to change. The latter may be directly related to the former. The southern grayling had both characteristics. Man-caused changes are so rapid that species do not have time to adjust genetically; adaptation must be within the existing genetic framework. If a wide genetic base is absent, the species can be expected to die-off over much of its range. Species that have been isolated as small populations in areas of uniform environment lack genetic diversity (Figure 18). Disjunct relict populations require a more specific habitat than populations in the center of the species range. The disjunct population may therefore have a more restricted habitat than other ecologically associated species.

Invaders can easily get a foothold in disturbed habitats because forces acting against grayling may be enhancing the position of a competitor. Climatic change, habitat change, and fishing pressure are not only negative for grayling but, also positive for a competitor.

It is essential to consider the stringent ecological requirements of grayling in regard to its decline. The grayling has to compete with those species that occupy headwater and lowland sections of the stream (Figure 19). Species that can live and reproduce under a wide variety

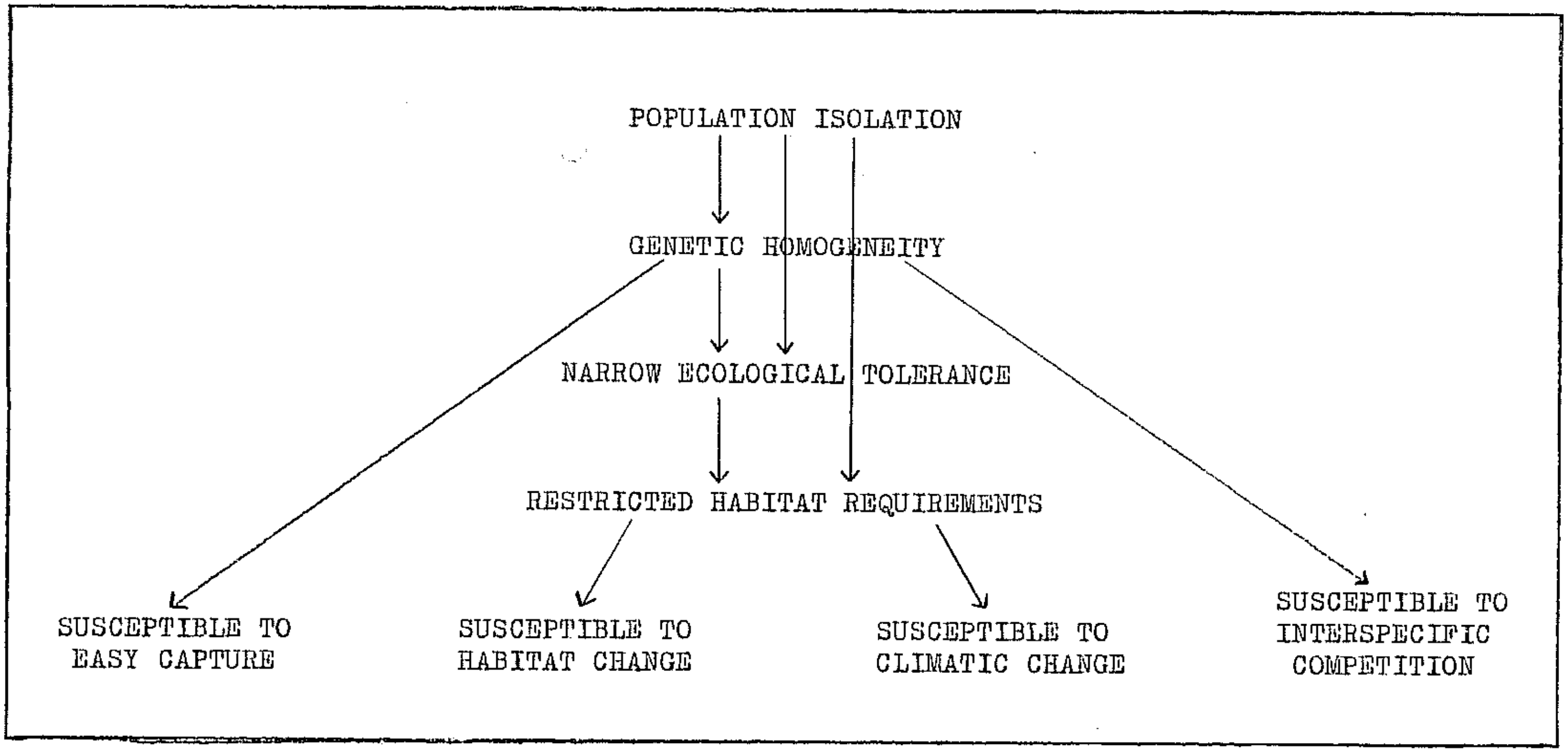

Figure 18.—The relationship of population isolation to susceptibility to change as suggested by the southern grayling populations.

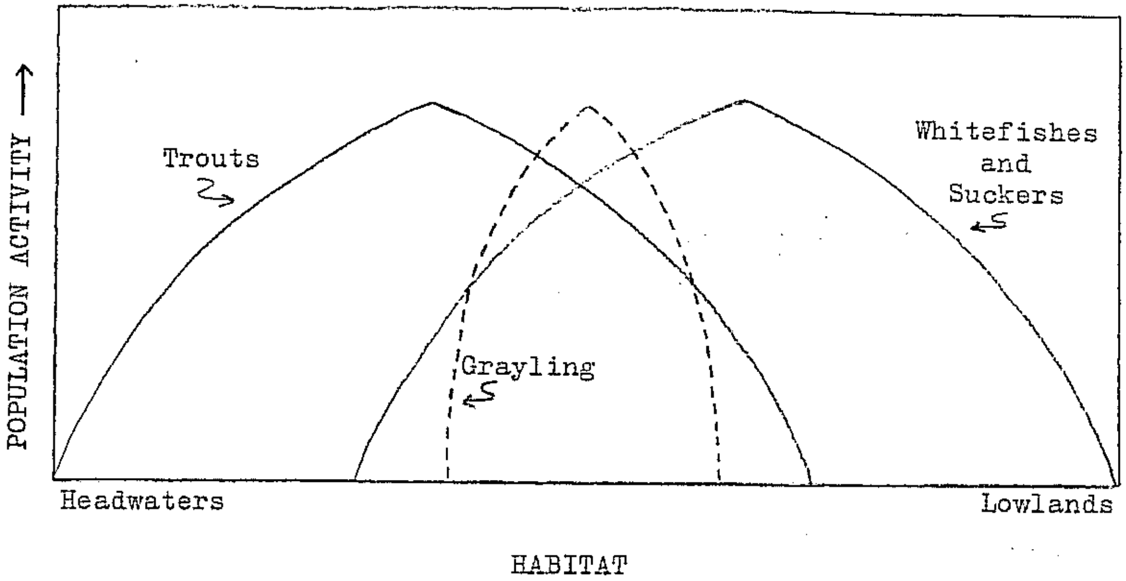

Figure 19.—A diagram showing that the narrow habitat range of grayling is nearly as optimum for headwater and lowland species as it is for grayling.

of water and substrate conditions usually persist the longest under changing environments (Langlois, 1941). Grayling competitors with a wider ecological tolerance hold the advantage. Therefore, because of climatic and habitat change, the grayling has lost its physical niche in most streams. Migration is precluded from a disjunct segment of the range, and habitat change is too rapid for genetic adaptation.

Topographic and stream characteristics that are necessary to form grayling habitat have features that also tend to make the habitat unstable. Recently deposited alluvial soils on deltas and valley floors are susceptible to erosion; stream meanders greatly increase bank erosion; large trees with well developed root systems are frequently absent from the stream bank; and relationship between stream-bed particle size and water current is delicate. In addition, man's demand is great upon these same local areas for agriculture, cities, dam sites, highways, or other cultural uses.

Although climatic conditions have been approaching a threshold, it seems that man-caused factors have become critical before water temperature or drought. In arid southwestern America, Miller (1961) concluded that man's direct or indirect disturbance of the environment has been the major factor in the depletion of fishes, not cyclic climatic changes.

Of the four possible major causes of grayling decline discussed in this study, three are due to man's activities and only one, climatic deterioration, would occur if man were not present. We can hardly consider man as an unnatural phenonemon, but it was his artificial actions (exploitation, introduction of exotics, and habitat change) that brought about the immediate range adjustment of grayling. Thus, although the stage was set by climatic change and the consequent disjunct populations, it was directly or indirectly man who played a major role in the decline of grayling in Michigan and Montana.

During the era of log driving in Michigan and diverting of small tributaries in Montana, few people realized that their activities were exterminating a resource. At the present there is little excuse for unawareness of the ramifications of land- and water-use practices. Nevertheless, at times the public has a poor opportunity to evaluate intelligently the alternative or the compatible uses. Certainly as a rule the presence or absence of a comparatively minor fish species will not deter the development of a large irrigation project or the logging of vast stands of timber. However, where feasible, substitute habitat should be provided for the deprived species either by stream habitat improvement or by transplanting the fish to an alternative river or lake that contains adequate habitat. For example, the latter can be applied in Montana where high altitude lakes are suitable grayling habitat and conflict with other use is at a minimum. Equally important is the encouragement of a species that is tolerant of new environments instead of attempting to maintain artificially a non-adapted species.

An inviolate river classification could be an essential tool of the regional and resource-use planner. Under such a system rivers would not need to remain in a primitive state but an environment would need to be maintained that supports a specific level of aquatic life. Land-use and watershed projects do not always enhance stream values (Alexander, 1960), and unquestionably they change the pattern of stream use. Therefore, what is deemed by man as desirable for the land is not necessarily best for rivers and their inhabitants.

It does not seem advisable to make a large-scale attempt at extending the range of grayling through artificial propagation. Proper habitat is not available, and the grayling is not a desirable enough game fish to warrant high expenditures. The ease with which grayling is captured probably limits its survival in any waters that are subject to even moderate fishing pressure. This same trait may make grayling useful for put-and-take stocking where an immediate high return is the goal.

The position of grayling as a sport fish is maintained by its scarcity. The state of Montana may be taking the proper approach by managing a few widely scattered alpine lakes solely for grayling. It is not intended that everyone catch a limit of grayling whenever they wish, but it is intended for grayling to be available for the few discriminate anglers who wish to hike into a wilderness lake in order to catch a comparatively rare fish.

There certainly must be other areas of suitable grayling habitat in the Rocky Mountains, Sierra-Cascade Mountain complex, and possibly the upper Great Lakes region and the New England States. Small barren or rehabilitated cool-water lakes with the proper small inlet streams for spawning are potential grayling habitat. Competitors should be absent; land use, restricted; and angling, curtailed. After these requirements are met, careful attention should be given to the substrate and water velocity of the inlet stream and to the lake littoral zone. The concept of what constitutes optimum trout water should not be applied to grayling.

Since grayling cannot provide as much sport for anglers as other fishes, its value and popularity lie in its scarcity. It would be inadvisable to introduce the European grayling or even the arctic grayling. The presence of either of these genetic stocks would destroy the uniqueness of the southern populations.

The southern grayling is not in immediate danger of extinction. By careful management and discreet addition of more populations, this fish will exist for a long time. From its example we can expect the southern border of distribution of other fishes to shift northward under the pressures of climatic change and land use as aquatic habitats are becoming less favorable for some species and more favorable for others. The more intense the land and water use the faster and farther will be the range adjustment.

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