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GRAYLING OF GREBE LAKE, YELLOWSTONE NATIONAL PARK, WYOMING

By THOMAS E. KRUSE

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CONTENTS

ABSTRACT

This is a study of certain features of the grayling population in Grebe Lake (near the center of Yellowstone National Park) fundamental to its management as a recreational resource. Field work was done in the summers of 1952, 1953, and 1954.

Grebe Lake is an eutrophic body of water at an elevation of 8,000 feet. It has an area of 145 acres and a maximum depth of 32 feet. The lake was covered with ice 6½ months annually; the highest surface temperature recorded was 67° F. Predominant insects by volume and number were the Tendipedidae (=Chironomidae), larvae and pupae. By July 14, 1953, an oxygen deficiency in the waters below a depth of 20 feet made them unsuitable for fish life. The grayling was introduced in the lake in 1921. Rainbow trout were planted in 1907, and cutthroat trout in 1912 (only hybrid trout are present now).

In the population estimates of 1953–54 trap nets were utilized along with a mark-and-recapture method. Approximately 28,000 grayling were in the lake in 1953 and 27,000 in 1954. The population of hybrid trout was estimated at 2,000 in 1953 and 2,500 in 1954. The standing crop of fish in Grebe Lake each year approximated 81 pounds per acre of which 73 pounds per acre were grayling and 8 pounds per acre were trout.

Both the grayling and the hybrid trout spawned in all four tributaries and in the outlet of Grebe Lake between mid-May and late June. The number of grayling spawning in 1953 was 7,081 and in 1954, 7,878. Enumeration of the trout at the same times showed 674 and 405, respectively.

During 1954 the natural fry production of grayling in the tributaries of the lake was estimated as 236,500 or 2.5 percent of the estimated number of eggs produced by the spawning adults. The greatest cause of mortality during the early developmental period was attributed to dislodgment of the eggs either by subsequent spawners or by changes in water level.

The time of annulus formation for grayling younger than 3 years was prior to June 25. Accurate interpretations of age from scales of grayling after their third year was impossible because of the small annual growth both in body and scale lengths. An additional complication often resulted from an absence of a scale annulus to designate the first year of life. This occurred on fish that were too small to have had scales at the start of their second growing season. The grayling reached the legal size of 6 inches during its second summer of life and matured during its third year of life.

The hybrid trout grew slower than the grayling during its first three years, but faster after age 3. The legal size (6 inches) was attained either in the second or third year of life. Some males of age-group II had matured, but no females matured until they were 3-year-olds.

Neither the grayling nor the trout was predatory. The food of the grayling during its first year consisted of small nymphs of aquatic insects, amphipods, and *Daphnia*. The major item in the diets of adults of both kinds of fishes was found to be Diptera larvae and pupae.

Fishing pressure on Grebe Lake was light with a harvest of only 7.1 percent of the estimated population or 6 pounds per acre in 1953, and 9.9 percent or 8 pounds per acre in 1954.

The combined mortality from anglers and predators in 1954 approximated 4,200 fish or 14.2 percent of the estimated adult population of 29,500 fish.

GRAYLING OF GREBE LAKE, YELLOWSTONE NATIONAL PARK, WYO.

By Thomas E. Kruse, *Fishery Research Biologist*, BUREAU OF SPORT FISHERIES AND WILDLIFE

The holarctic grayling, *Thymallus arcticus* Pallas, is one of the rarest North American game fishes. Its localized distribution on this continent, as well as the great beauty of the fish, have focused the interest and concern of ichthyographers and sportsmen on the species.

The first specimens to be collected in America were from Winter Lake near Fort Enterprise (Northwest Territories) and were identified by Sir John Richardson who called them Back's grayling (Franklin 1823). The grayling was subsequently found in Michigan and Montana and in many streams of Alaska and Canada eastward to the western shore of Hudson Bay. This distributional pattern was evidently the result, first, of glacial action which extended the range southward, and second, of later habitat changes which left only two relict populations south of the Canadian border.

The grayling of North America is conspecific with the Asiatic form, *Thymallus arcticus* Pallas (Walters 1955; Wilimovsky 1954). Walters (1955) further recognizes for North American individuals the subspecies *signifer* (for Alaska and Canada specimens) and *tricolor* (for Michigan-Montana individuals).

In Eurasia, *Thymallus arcticus* occurs from the Ob system of western U.S.S.R. to the eastern Siberian Coast (including all streams draining into the Bering Sea and the Penzhina River draining into the Sea of Okhotsk), and south to the Baikal basin, Sea of Japan basin, and the Yellow Sea basin (Yalu River) (Walters 1955).

In Canada and Alaska the grayling is found in the Arctic Ocean drainages, and from the Bering Sea drainages and the Alsek River and Stikine system of Pacific Coast drainages, east to the western shore of Hudson Bay. The southern limit is the headwaters of the drainages concerned and south along the west shore of Hudson Bay to just north of the Nelson system in Manitoba (Walters 1955).

In the United States, the grayling was indigenous to the following two areas: (1) the upper part of Michigan's Lower Peninsula, and in the Otter River of the Upper Peninsula (Hubbs and Lagler 1949), and (2) headwaters of the Missouri River above the Great Falls in Montana (Henshall 1902).

In Michigan, the grayling is a fish population of the past. Its disappearance has been attributed to many factors. Those most often cited are logging drives during the spawning season, competition with other species, deforestation and consequent rise in water temperatures, and fishing pressure. Streams such as the Manistee River, where the grayling was once so abundant that two men and two women were reported to have caught 3,000 individuals in 14 days and to have hauled 2,000 of them to Chicago, are now barren of the species (Creaser and Creaser 1935).

Transplantations from Montana have met with little success in distant States. Somewhat better results have been attained by stocking within the State itself. Grayling introduced into Georgetown Lake and Rogers Lake, Mont., for example, supplied for many years the majority of spawn taken for fish cultural purposes by the Montana Game and Fish Commission (Moffett 1950). However, even within Montana the range of the grayling has decreased. It is rarely observed in the Madison River drainage and is absent entirely from the Missouri River, the Gallatin River, and the main stem of the Jefferson River. The only indigenous population maintaining itself at present is in the Red Rock Lakes region of the Beaverhead drainage, where its management was studied by Nelson (1954).

Foremost among the individuals who have studied the grayling is Dr. C. J. D. Brown (1938a, 1938b, 1939, 1943) who did research on age and growth, food habits, habitat, and spawning behavior. Watling and Brown (1955) investigated the early embryology of the grayling. Moffett (1950) reported briefly on the status of the grayling in Grebe Lake.

NOTE.—Approved for publication July 8, 1958. Fishery Bulletin 149.

Creaser and Creaser (1935) made a comparative analysis of age and growth of the Michigan and Montana varieties. Leonard (1939a, 1939b, 1940, 1949) recorded a number of observations in Michigan on stocks transplanted from Montana. Miller (1946), Rawson (1950), and Ward (1951) increased our knowledge of the species by life-history studies on the grayling in Canada. Wojcik (1955) also made a life-history investigation of the grayling in waters of interior Alaska.

In Yellowstone National Park, Wyo., the grayling occurred naturally in the Madison River and its tributaries, upstream to major barriers such as the Kepler Cascades on the Firehole River and Gibbon Falls on the Gibbon River. Transplants within the Park have produced varying results. Both North and South Twin Lakes provide good grayling fishing for small fish, but the population depends on regular stocking because there is no natural reproduction of the species. The most successful introductions have been those in a series of three lakes (Grebe, Ice, Wolf), formerly barren of fish life, above Virginia Cascades on the Gibbon River. Grebe and Wolf Lakes are a direct part of the Gibbon River system which drains into the Madison River, and Ice Lake is a few hundred yards from the main river on a small tributary. A fourth grayling lake, Cascade, lies close to the other three but is in the drainage of the Yellowstone River.

An alarming decline in numbers of the grayling in Grebe Lake occurred in 1948 and 1949. To rectify this, the National Park Service, responsible for preserving and maintaining the present stock of grayling in Yellowstone Park, believed that technical management measures were necessary, but basic biological data on the species and on Grebe Lake were lacking. This study, under the auspices of the U. S. Fish and Wildlife Service, was aimed at providing a scientific basis for the management of the fisheries of Grebe Lake.

I wish to thank Dr. Karl F. Lagler, Department of Fisheries, University of Michigan, for guidance during this study and for critically reviewing the manuscript. Field research was supervised by Dr. O. B. Cope, Chief of the Rocky Mountain Sport Fishery Investigations; equipment and funds were provided by the U. S. Fish and Wildlife Service.

ENVIRONMENT

PHYSICAL CHARACTERS

Grebe Lake lies at an elevation of approximately 8,000 feet on Solfatara Plateau near the center of Yellowstone National Park. This 145-acre lake is contained in a circular basin. The volcanic sand bottom is overlain by a blanket of muck (decomposed organic matter and silt) about 1 foot thick. The prevailing westerly winds have formed, through wave action, a narrow sandy beach on the eastern side of the lake. A maximum depth of 32 feet was found near the southeast shore (fig. 1). At the outlet, remnants of a beaver dam have raised the water level about 1 foot and formed a shallow curving arm 50 feet wide and 300 feet long.

Four major inlets enter Grebe Lake. These quickly break up into many small, spring-fed tributaries upstream from the lake. In addition, seepage areas contribute their flow, particularly during the moist spring and early summer. The outlet (Gibbon River) flows to the west and empties into Wolf Lake (42 acres) about 1 mile downstream from Grebe Lake. From there the stream travels 15 miles westerly to unite with the Firehole River and form the Madison River. Four miles below Wolf Lake a 50-foot cascade prevents any fish below the barrier from entering the waters above (the Grebe Lake system).

Temperatures at the surface and on the bottom of Grebe Lake were recorded continuously by a Brown thermograph (fig. 2) placed near the deepest area in the lake. Spring overturn occurred during 1953 on or about the third day after the ice completely left the lake. By July 1 the lake had stratified thermally. Maxima of average weekly surface temperatures (hourly interpretations) were reached in 1953 and 1954 between July 16 and 30 (fig. 3). Temperatures were still increasing at the bottom when the thermograph was removed from the lake on August 27, 1953.

The highest daily temperatures were 65° F. (at the 6-ft. level) on July 20, 1953, and 67° F. (1-ft. level) on July 13, 1954. Daily surface maxima occurred in the afternoons (between 1:00 and 5:00 p. m.) throughout the season. A surface minimum of 41° F. was recorded May 12, 1953. The daily range never exceeded 3° F.

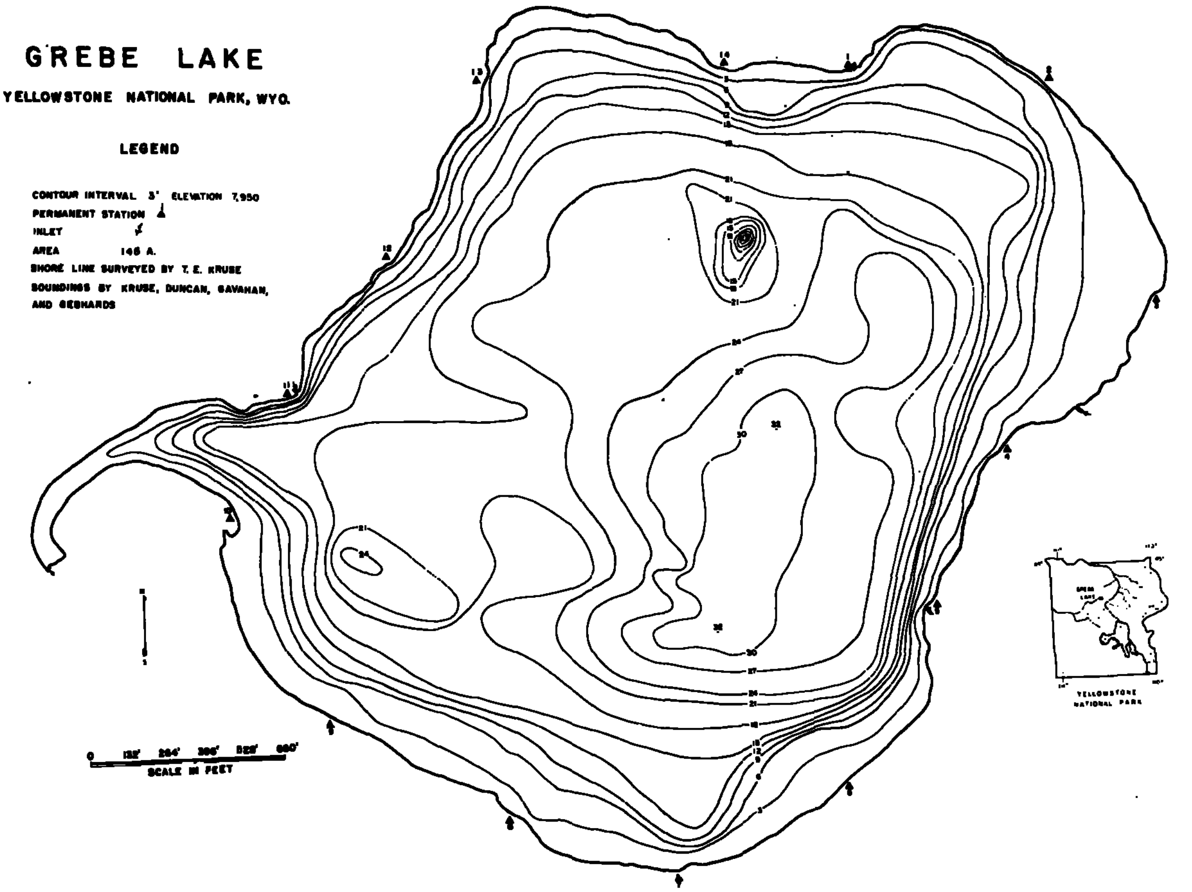


FIGURE 1.—Contour map of Grebe Lake, Yellowstone National Park, Wyo.

during 1953 (6-ft. depth) or 4° F. in 1954 (1-ft. level).

Thermal characteristics of Hatchery Creek, one of the inlets, were also recorded by a thermograph in 1953 and 1954 (fig. 4). Average weekly temperatures rose rapidly during June, then, gradually until mid-July. The maximum hourly temperature of 63° F. occurred at 3:00 p. m. on June 18, 1953. The daily peak was reached between 1:00 p. m. and 5:00 p. m. Daily minima occurred between 5:00 a. m. and 7:00 a. m. The greatest range for a 24-hour period was 23° (June 17, 18, 1953). The highest temperatures occurred in late spring and resulted from floodwater, which flowed in a shallow layer over the meadow surrounding Hatchery Creek, then drained back into the creek bed above the thermograph.

CHEMICAL FACTORS

Grebe Lake stratified both thermally and chemically during 1953 and 1954. On July 14, 1953, grayling and hybrid trout taken from trap nets set in water more than 20 feet deep were dead or in distress when the nets were lifted, but not so for those in shoal sets. The results of a water chemistry analysis made August 6, 1954, showed that the oxygen concentration in the lake at the 20-foot level contained only 4.5 p. p. m. (54.4 percent saturation) and decreased to 0.6 p. p. m. (6.8 percent saturation) at a depth of 28 feet (table 1).

Grebe Lake may be classified as an eutrophic lake with a deficiency of oxygen in its depths during the period of summer stagnation.

BIOLOGICAL FEATURES

Three species of plants dominated the vegetation within the lake. Large beds of waterlilies, *Nuphar polysepalum*, paralleled the eastern shoreline and extended into the lake up to 100 feet. On the bottom between water depths of 4 feet and 15 feet laid a nearly continuous 2-foot blanket

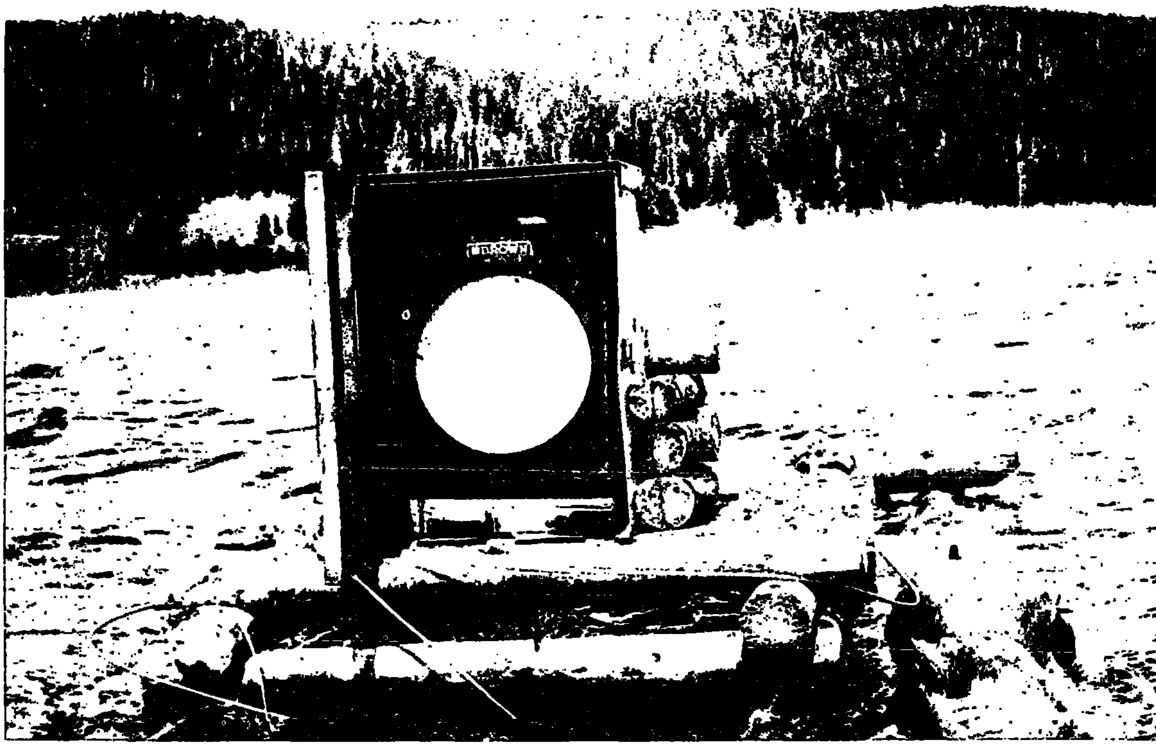


FIGURE 2.—Brown thermograph and log raft as they appeared in Grebe Lake, July 1954.

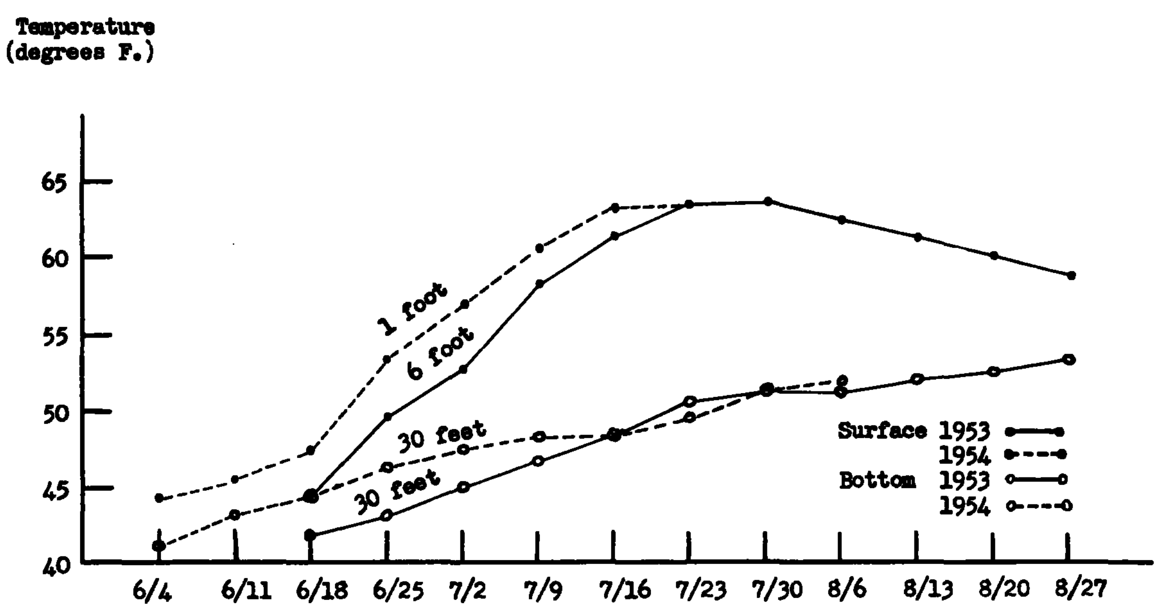


FIGURE 3.—Average weekly water temperatures (hourly observations from thermograph records) for Grebe Lake, Yellowstone National Park, Wyo., during 1953 and 1954.

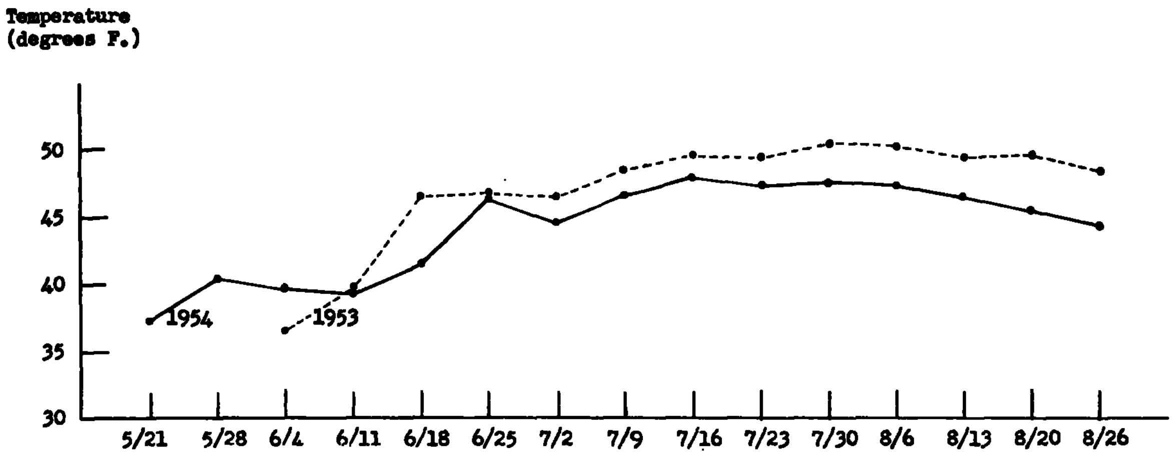


FIGURE 4.—Average weekly water temperatures (hourly interpretations from thermograph records) for Hatchery Creek, tributary of Grebe Lake, Yellowstone National Park, Wyo., during 1953 and 1954.

of *Potamogeton robinsii.* Through this dense cover grew scattered patches of another pondweed, *Potamogeton amplifolius.*

Bottom fauna was sampled with an Ekman dredge (6 ins. by 6 ins.). Standardized collections with the equipment available were possible only on bottom without a vegetative cover at depths above 15 to 18 feet. Two of the samples were collected in shallow areas less than 18 feet where only vegetation was retained by the dredge. The organisms were rinsed from the plants and enumerated for (1) general type and (2) relative abundance (table 2). Twenty-three samples from the open water of the lake were analyzed.

TABLE 1.—*Physical and chemical features of Grebe Lake on Aug. 6, 1954*

Location	Temperature (degrees F.)	Free CO_2 (p. p. m.)	pH	M. O. alkalinity (p. p. m.)	O_2 (p. p. m.)	Percent saturation
Lake surface	62	5.0	7.2	14.0	7.6	104.7
5 feet	62	4.5	7.6	18.0	7.4	102.0
10 feet	61	3.5	7.6	17.0	6.8	92.5
15 feet	60	5.0	7.2	18.0	5.4	73.4
20 feet	53	12.0	6.4	18.0	4.5	54.4
25 feet	50	21.0	6.4	17.0	1.6	19.0
28 feet	50	16.0	6.4	17.0	.6	6.8
Outlet	58	4.0	7.2	18.0	8.8	115.6

Tendipedidae (=Chironomidae) were the most important bottom organisms at all depths, both in numbers and by volume (table 2). Forbes' (1893) collections from Grebe Lake, taken before fish had been introduced, included the following forms: (from the bottom), *Chironomous, Gammarus, Pisidium, Diaptomus lintoni, Daphnia clathrata,* and *Cyclops;* (from inshore samples), *Gammarus, Allorchestes, Pisidium, Corisa, Physa, Chironomous, Spongilla, Nephelis, Clepsine,* Ephemeridae, Odonata, and *Haliplus.*

TABLE 2.—*Qualitative analysis of bottom fauna from Grebe Lake, 1952*

Organism	Depths greater than 15 feet (23 samples)			Plant rinses [1] (2 samples)		
	Number	Volume (cc per sq. ft.)	Percent volume	Number	Volume (cc per sq. ft.)	Percent volume
Nematoda	96	0.40	1.71	1	T	--------
Oligochaeta	1,352	2.80	11.97	25	0.05	2.38
Gastropoda	8	T	--------	43	T	--------
Pelycopoda	1,056	4.00	17.09	--------	--------	--------
Hydracarina	--------	--------	--------	1	T	--------
Ephemeroptera	--------	--------	--------	3	T	--------
Anisoptera	--------	--------	--------	1	.40	19.05
Trichoptera (case)	8	.20	.85	2	1.00	47.62
Tendipedidae (= Chironomidae)	1,744	16.00	68.38	1,736	.65	30.95

[1] Each sample was arbitrarily the amount of vegetation which filled a 2-quart jar without packing.

HISTORY OF FISH IN GREBE LAKE

In 1907, 10 cans of eggs of rainbow trout (*Salmo gairdneri*) were planted in Grebe Lake (annual reports of Superintendents of the Yellowstone National Park, 1908). In 1912, 300,000 fry of cutthroat trout (*Salmo clarki lewisi*) from Yellowstone Lake were introduced (record cards in Chief Ranger's Office, Yellowstone National Park). Since that time the two salmonid species have hybridized to such an extent that by 1952 no fish were found which were definitely pure strains of cutthroat or rainbow trout. The hybrids have the general appearance of rainbow trout, but with a red slash on each side of the hyoid membrane. Hyoid teeth, a cutthroat characteristic, were present in all specimens examined. Body forms range from the typical elliptical shape of the cutthroat to the blunt, stocky, high-shoulder outline of the rainbow.

TABLE 3.—*Annual removal of grayling eggs and stocking of Grebe Lake, 1931–54*

[Moffett, 1950; stocking records are in Chief Ranger's Office]

Year	Number of eggs	Eggs or fry returned to lake
1931	750,000	750,000
1932	768,000	[1] 40,000
1933	2,118,400	650,000
1934	4,443,000	735,000
1935	3,660,000	676,500
1936	4,211,140	400,000
1937	5,715,000	1,000,000
1938	5,837,000	384,635
1939	5,117,368	80,000
1940	4,660,209	1,009,410
1941	5,019,403	1,120,631
1942	4,093,589	1,021,000
1943	3,300,000	484,584
1944	1,774,784	None
1945	1,787,336	None
1946	1,746,324	153,018
1947	2,178,155	None
1948	4,217,464	None
1949	1,758,155	225,000
1950	1,653,845	500,000
1951	(2)	300,000
1952	(2)	300,000
1953	1,708,910	400,000
1954	428,800	350,000

[1] Remainder lost.
[2] Data on spawntaking activity is unavailable for these years.

Grayling were first planted in Grebe Lake in 1921, when a million eggs were brought from Anaconda, Mont. (record cards in Chief Ranger's Office, Yellowstone Park). The species was gradually established in the lake and by 1930 large spawning runs were observed in the various inlets. In 1932 a few eggs were taken artificially on an experimental basis for hatching by the U. S. Bureau of Fisheries. Results were so encouraging that a permanent hatchery was established at the lake. In 1933, more than 2 million eggs of this species were taken from Grebe Lake (Leach, 1934–35). Region II of the U. S. Fish and Wildlife Service and particularly the Park itself received most of the fish produced. The yearly take of eggs and return of eggs and fry to Grebe Lake (table 3) show how well the species established itself. An extremely low population occurred in 1949 when so few spawning fish entered Hatchery Creek weir that only a portion of the grayling egg commitments by the fish culture station could be filled. The lake was then closed to fishing; and restocking, which had been rather neglected for the previous 5 years, was undertaken vigorously.

RECENT POPULATIONS IN GREBE LAKE

Knowledge of population size and composition (year-class and species) are fundamental to the prediction of angling success. Since the Grebe Lake problem involved species interaction, knowledge of population size was particularly important.

POPULATION ESTIMATES

Populations of grayling and trout were approximated by the Schnabel (1938) formula as modified by Chapman (1952). With a population estimate of this type, fish are captured in successive time units, unmarked fish are marked, and all individuals are released. The ratio of tagged fish (s) to total captures (n) in any sample provides an estimate of the ratio between the total number of tagged fish in the population at the time of the sample (t) and the total population (N). As the numbers of marked fish in the population increase during the experiment, the ratio of s/n also increases subject to sampling errors. Schnabel used the method of maximum likelihood to combine these sequential estimates into single weighted mean such that $N=\frac{nt}{s}$.

Chapman (1952) stated that for an unbiased estimate of the true population the formula should be $N=\frac{nt}{s+1}$. With the use of either the Schnabel formula or this modification the author indicated that the confidence interval on N could be determined from the Poisson approximation given by Chapman (1948).

In 1953, the equipment used for the population study consisted of 5 impounding nets. Two were fyke nets on hoops 3½ feet in diameter; each unit was 12 feet long, was made of 1-inch mesh (mesh sizes are stretched mesh), and had two throats. Each net was also equipped with 12-foot wings but no leader. The third hoop fyke net was 4 feet in diameter, 15 feet long, and of 2-inch mesh. The wings were 50 feet in length and were made of 2½-inch mesh. The remaining equipment consisted of 2 trap nets (much as shown by Crowe, 1950) having a pot, heart, and wings. The pot was of 1-inch mesh and the heart and wings were of 2½-inch mesh. When set, such units tapered from the wings which were 20 feet apart at their outermost end, to the pot which was 5 feet wide by 8 feet long by 3 feet deep. All the net gear was soaked in dark-green, copper naphthanate.

In 1954, four trap nets and a seine were used to capture the fish. Two trap nets were those used during 1953. Two new units were identical with the 1953 design except for a smaller mesh size (1½-ins. rather than 2½-ins.) in the wings. Leaders were not used. These new nets were preserved with light-green copper napthanate. The tied seine was 75 feet by 4 feet, with 1-inch mesh.

In the population studies, both trout and grayling were taken from depths up to 30 feet. The first sets made in deep water (more than 20 feet) killed all the fish that entered the impounding nets. Subsequently only the shallow portions of the lake (less than 20 feet deep) were fished. These shoal areas were sampled randomly by dividing a map of the lake into a grid pattern, numbering the intersections, and drawing numbered slips of paper to determine the sites. Nets were set, lifted each morning, moved to the next predetermined location, and reset. The few shallow areas where seining was possible were fished 9 times at night during the 21-day sampling period in 1954.

Captured fish were held in a floating live box attached to a boat. The seined fish were towed to the approximate center of the lake, fin-clipped, and released. Fish from nets were distributed around the lake as the boat moved from one net location to the next. The left pectoral fin was removed in 1953 and the right pelvic fin in 1954. Only grayling in their third year of life (longer than 8.4 ins.) and older, and trout more than 5 inches in length, were marked in 1954. The previous year all fish captured were marked (minimum size 4.3 inches for grayling, 3.3 inches for trout).

The period of netting extended from July 8 to August 9 (33 days) in 1953, and from July 1 to July 21 (21 days) in 1954.

To determine the most effective direction to face nets and capture grayling and hybrid trout, 30 sets were placed randomly. The results of the collections (table 4) showed that traps facing the shore were two to five times as effective as those directed toward the center of the lake or parallel to shore. An analysis of variance between numbers of fish captured during various facings indicated significance at the 5-percent level.

In the evening feeding period, the grayling and hybrid trout were evenly distributed about the lake, as judged from patterns of rises. For trout, this conclusion was substantiated by net captures. However, net locations along the outer border of the lily pads and in the shallow eastern portion (fig. 5) consistently resulted in more grayling captures than those in any of the other areas (table 5).

In 1953, the average daily catch in nets during the 33-day period was 40 fish (table 6). The trap nets were the most effective gear in this operation. These two units accounted for 983 (74.5 percent) of the 1,320 fish taken. By species, the trap nets took 21.5 percent (284) of the hybrid trout and 78.5 percent (1,036) of the grayling. Angling added 209 grayling and 67 trout to the marked population with 6 grayling and 4 trout recaptured by this means.

The greater effectiveness of trap nets over fyke nets in total catch of fish (fig. 6), and the difference in sizes of individuals captured in the two types of

TABLE 4.—*Numbers of fish captured by 30 net sets faced randomly in Grebe Lake in 1954*

Catch	Direction of net					
	Perpendicular, toward shore		Perpendicular, away from shore		Parallel to shore	
	Trout	Grayling	Trout	Grayling	Trout	Grayling
Number captured	47	256	7	25	13	102
Average catch per set	3.6	19.7	1.0	3.6	1.3	10.2
Number of sets	13		7		10	
Total catch per set (both species)	23.3		4.6		11.5	

TABLE 5.—*Fish concentrations in various parts of Grebe Lake as determined by net captures (1954 data)*

Area	Total catch		Number of sets	Catch per set		Overall average catch per set
	Trout	Grayling		Trout	Grayling	
Eastern shelf	62	254	17	3.65	14.94	18.59
South shore	29	79	10	2.90	7.90	10.80
Lily pads	72	607	36	2.00	16.86	18.86
Northwest shore	13	40	5	2.60	8.00	10.60
North shore	42	148	14	3.00	10.57	13.57
Total	218	1,128	82	2.66	13.76	16.41

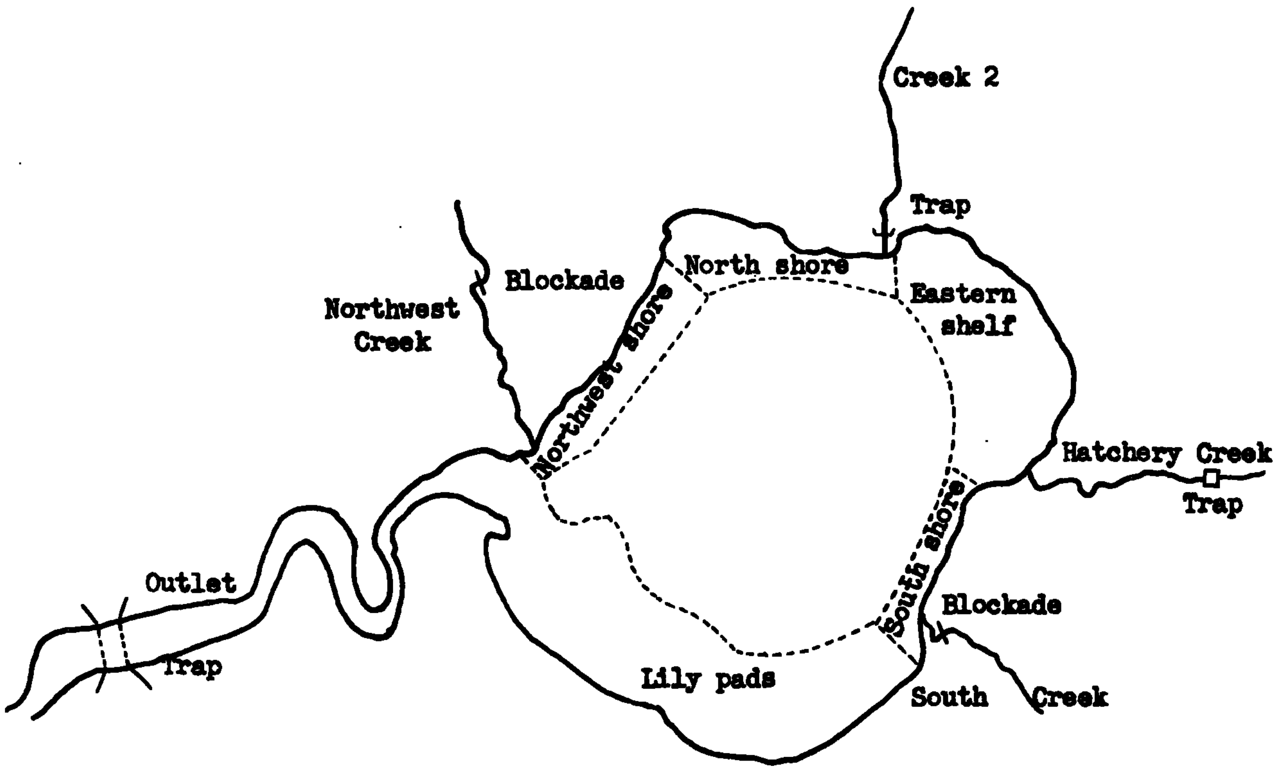


FIGURE 5.—Diagrammatic map of Grebe Lake, Yellowstone National Park, Wyo., showing tributaries, spawning barriers, and lake divisions used in netting analysis.

gear resulted in the sole use of four trap nets in 1954 plus some seining at night.

TABLE 6.—*Catch of trout and grayling in different types of nets during the Grebe Lake population study (July 8, 1953–Aug. 9, 1953, and July 1, 1954–July 21, 1954)*

		Average daily catch [1]			Total catch		
Year	Species	Trap nets	Fyke nets	Total	Trap nets	Fyke nets	Total
1953	Trout	6.8	1.8	8.6	224	60	284
	Grayling	23.0	8.4	31.3	759	277	1,036
	Combined	29.8	10.2	40.0	983	337	1,320
1954	Trout	10.4	[2] 19.3		219	174	393
	Grayling	53.9	25.0		1,132	225	1,357
	Combined	64.3	44.0		1,351	399	1,750

[1] Daily catch in various types of nets (2 trap nets, 3 fyke nets in 1953 and 4 trap nets plus seine in 1954).
[2] Daily average of the 9 days on which the seine was used.

The best results in 1954 were obtained with the two trap nets with a mesh size of 2½ inches in the wings. These two nets were 3.5 times as successful as the small-meshed units of the same design. However, the two nets with 1½-inch mesh wings were treated with a light-colored preservative (copper naphthanate); the other two were more darkly stained in the preservation process. The total catch of fish in trap nets in 1954 was 1,351 for an average daily catch of 64.3 over a 21-day period (table 6). Fish seining on nine occasions during the mark-and-recapture period took 174 trout (44 percent of total trout captures) and 225 grayling (17 percent of total grayling captures).

The population (fish more than 4.3 inches total length for grayling and 3.3 inches total length for hybrids) for Grebe Lake for 1953 was estimated to be 28,956 fish or 77.3 pounds per acre (table 7). In 1954, a comparable Schnabel-type estimate for grayling over 8.4 inches and hybrids of more than 5.7 inches was 28,430 fish or 79.2 pounds per acre.

TABLE 7.—*Population estimates for Grebe Lake, 1953, 1954*

Year	Species	Number captures	Recaptures	Estimated population	Confidence limits 95 percent [1]		Estimated weight [2] pounds per acre
					Upper	Lower	
1953	Trout	353	24	2,041	3,164	1,343	7.1
	Grayling	1,251	22	26,915	42,652	17,370	70.2
1954	Trout	393	24	2,548	3,949	1,676	8.3
	Grayling	1,357	30	25,882	38,111	17,820	[3] 70.9

[1] Confidence limits from table 1, Chapman (1948).
[2] Weight determined from length-weight relation by converting fish lengths in nets to weights of fish in nets and then assuming a proportional relation between number of fish in nets and Schnabel estimate.
[3] Pounds per acre of grayling increased in 1954 because of the larger size of fish the second year (average size 10.5 inches in 1953, 11.0 inches in 1954.).

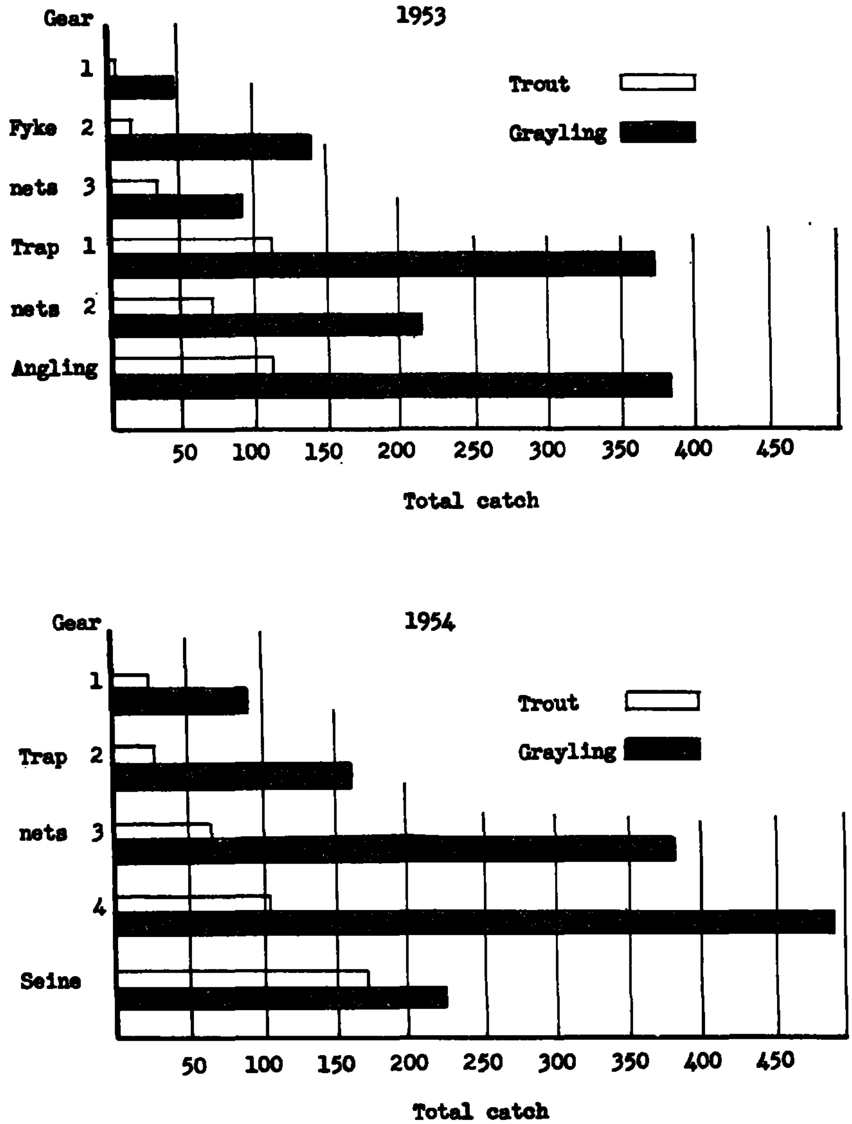


FIGURE 6.—Effectiveness of gear in capturing hybrid trout and grayling in Grebe Lake during the mark-and-recapture study, 1953 and 1954.

Methods of forming population estimates which have been used by biologists and the prerequisites necessary for the use of various methods have been adequately discussed by Ricker (1948), DeLury (1951), Cooper and Lagler (1956), and others. It is essential, however, to indicate which of these prerequisites have and have not been fulfilled by this study and hence what reliability can be placed on the estimated numbers of trout and grayling.

The first assumption of a mark-and-recapture study is that either (1) marked fish distribute themselves randomly throughout the lake, or (2) that the fish are captured by a random placement of the nets proportional to the population density in different parts of the lake. Nets in this particular study were set randomly and fish captured were redistributed in various parts of Grebe Lake to ensure randomness.

Secondly, mortality among the marked fish must not be greater than among unmarked individuals. The result of such an error would be a decrease in the marked specimens and a population estimate that is too large. Ricker (1949) was unable to demonstrate significant mortality in a population of fish from which one fin had been removed, and no visible evidence of excessive mortality was observed by me. Frequently some fish were weakened by handling and swam near the surface in the live box. When released, these individuals remained visible from the surface and became targets for osprey after the boat left the area for the next station. Such fish, visibly weakened, were never marked. In 2 years, only one dead marked fish was found.

A third assumption is that recruitment is negligible during the time recoveries are being made. Recruitment contributed both trout and grayling to the 1953 population, biasing estimates upward. Although all grayling which were sampled during the first year were at least in their second summer of life, the smallest 2-year-olds (less than 4 inches) undoubtedly passed through the finest mesh (1½-inches), at least for the first part of the recapture period. The 1953 nettings captured no grayling between 7.4 inches (largest 2-year-olds) and 8.8 inches (smallest individual more than 2 years old). To minimize the effects of recruitment in 1954 only grayling more than 8.4 inches were marked.

Trout presented a different problem. In 1953, trout as small as 3.3 inches were marked, however, only 7 fish less than 5 inches were measured and these few trout captures were all that recruitment might have contributed to the marked population. This error was negligible. In 1954, although hybrids as small as 5 inches were to be marked, no trout less than 5.7 inches in total length were captured by the seine, or less than 6.1 inches by the nets. Since the 1954 gear would retain 5-inch hybrids, recruitment only slightly biased the 1954 estimates.

A fourth assumption is that no mortality, either natural or by fishing, acts to reduce the population during the recapture period. Grebe Lake was subject to light fishing pressure both years during the population study. Approximately 301 hybrids and 343 grayling were caught by anglers in 1953 and 275 trout and 472 grayling in 1954 during the marking period. Only four fin-clipped fish were reported by anglers in the 2 years. That some marks escaped the notice of fishermen, is probable, since of 290 fish caught by angling and marked by me in 1953 during the study, 10 of these were recaptures. Thus more than 3 percent of my captures had been marked, but only 0.3 percent were reported by anglers as fin-clipped. The result of mortality during this experiment undoubtedly increased estimates.

The fifth assumption is that there is no differential availability of marked and unmarked fish (that marked fish did not become "trap-shy" as a result of handling). A means of checking the number of recaptures by the net would be to sample the population by a means other than trap netting and compare the percentage of recaptures by the new method to results obtained from trap netting. Such samples were available in 1953 as personal angling, and during 1954 as seining. I was unable to demonstrate any significant difference between 1953 recaptures by nets and recaptures by fishing of either hybrid trout or grayling. In 1954, the ratio of marked to unmarked fish was greater in the seine than in the trap nets. A chi-square test indicated a significant difference at the 95 percent level between grayling recaptured in nets and recaptures by seining. Such evidence suggests that marked grayling avoid trap nets more frequently than unmarked individuals. The result of such differential availability in grayling was to increase the population estimate. Trout recaptures by the seine and by nets were not significant at the 95-percent level.

Of the estimated populations, 16 percent of the trout were captured in 1953 but only 4 percent of the grayling. Thus there is evidence that the trout are more susceptible to trap netting than are the grayling.

An additional error appeared in the 1953 estimate when the mean length was different for fish captured by the different types of gear (two small-mesh hoop fykes, two trap nets, and one large-mesh hoop fyke) (fig. 7). An analysis of variance (table 8) of these 1953 data indicated that this difference in mean lengths was significant at the 95 percent confidence limits. The various nets therefore sampled different parts of the population, and each did so with its own effectiveness. It was for this reason that four trap nets of a single design were used in 1954, but unfortunately all bias was not overcome because the two newer nets were preserved with a light-colored copper naphthanate and had a different mesh size in the wings.

An analysis of variance (table 9) showed that in 1954 the mean sizes of fish from the different trap nets were significantly different from one another and also from the seined sample. This meant that, despite precautions, again in 1954 the equipment was sampling different segments of the population. Possibly this resulted from using the fish captured in the twine of the wings of the two large-meshed trap nets; this larger mesh selectively retained larger fish.

The seine proved effective when used at night close to shore. Seined grayling averaged slightly smaller than those captured by trap nets. This size difference was also significant (table 9) for this species, but such a difference could not be demonstrated for trout.

TABLE 8.—*Analysis of variance of mean lengths of fish taken in 5 nets in 1953 population study on Grebe Lake*

	Sum of squares	Degrees of freedom	Mean square	F ratio
Means	288.06	4	72.01	$F_s = \frac{72.01}{4.24} = 16.98$
Within	1,644.97	388	4.24	F95 (4,388) = 2.37

The error associated with samples stratified by size will tend to increase population estimates. Such an error is common to most problems though unrecognized when only one type of equipment is

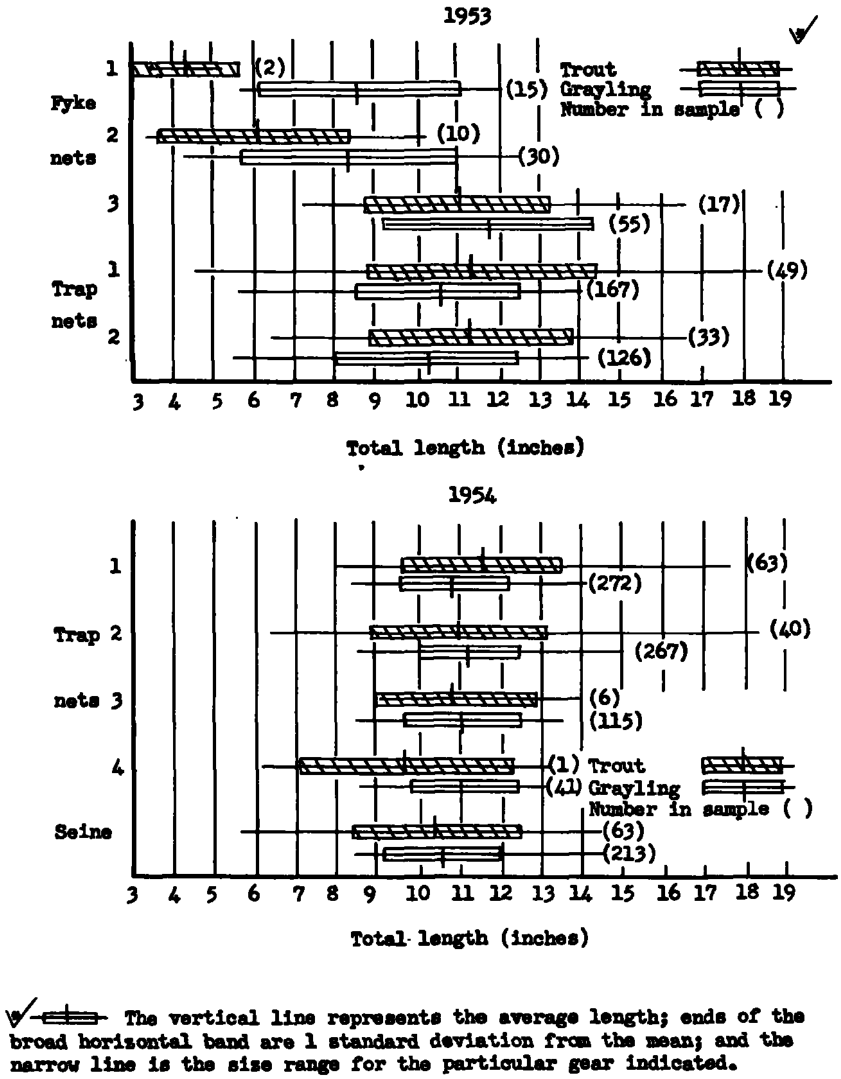


FIGURE 7.—Comparison of lengths of grayling and hybrid trout in individual nets and the seine during the 1953, 1954, population study on Grebe Lake, Yellowstone National Park, Wyo.

used. Ricker (1948) considered errors introduced through unequal vulnerability of fish of different sizes not to be serious.

TABLE 9.—*Analysis of variance of mean sizes of fish captured by various methods in 1954*

Method of capture	Species	Observed F ratio	F ratio (5-percent value)
Between 2 types of trap nets	Trout	F=2.97	F_{95} (3, 691)=2.68
	Grayling	F=3.33	F_{95} (4, 278))=2.37
Between small mesh trap nets and seine	Trout	F= .79	F_{95} (2, 177)=3.00
	Grayling	F=6.06	F_{95} (2, 366)=3.00

FACTORS CONTROLLING COMPOSITION OF THE GREBE LAKE POPULATION

SPAWNING OF GREBE LAKE FISHES

An initial determinant of fish population size is the reproductive success of its components. In the Grebe Lake system, ample spawning facilities appear to exist for both the grayling and the hybrid trout. Yet, in a search for factors limiting the abundance of the grayling (which fluctuates drastically) thought must be given to undesirable competition, and possibly to predation by trout on the spawning grounds that are shared in a very concentrated way with the grayling.

Most of the information on the spawning populations of fishes in Grebe Lake was obtained from weirs. One of these fish traps was on Hatchery Creek where grayling spawn has been collected annually since 1931. Additional weirs or blockades were installed in each of the tributaries of Grebe Lake and in the outlet (the Gibbon River) about 150 yards downstream from the lake (fig. 5).

In 1953, when the snow melted, the large volume of water from the surrounding mountains poured into the inlets, clogged the traps, and allowed many fish to bypass them. Only the installations on Hatchery Creek (fig. 8), the outlet (fig. 9), and South Creek withstood the high waters and enabled analysis of the spawning population. The weirs and blockades (fig. 10) installed in the Grebe Lake system in 1954 were more effective than those of 1953, since improvements had been made in construction and the spring runoff was spread over a longer period of time.

Spawning Areas

Grayling and trout spawn in all inlets and in the Gibbon River below Grebe Lake. The area of each waterway available for spawning was estimated by the following method. During the time of hatching and while fry were still present in the streams, the farthest upstream locations of fry were determined for each tributary. Measurements were then made from the first natural barrier above these fry to the lake. All distances were recorded by wading the creeks and measuring with a steel tape the distance traveled. On 3 of the 4 tributaries, greatest widths were taken at each 100-foot interval even to include undercut regions beneath banks. On the fourth, Northwest Creek, and on the Gibbon River, widths were measured every 357 feet.

The variability of bottom types and of currents made some sections unacceptable to spawning fish. In computing the amount of suitable spawning grounds, the sections between each width measurement station were evaluated separately and the results were combined to obtain totals (table 10). Visual estimates of suitability were based on: (1) type of bottom (best-to-worst: gravel, sand, and rubble), (2) speed of current (slow or medium current preferred to a fast velocity), and (3) general characteristic of the stream for that section (riffles attracted more spawning fish than did pools). In general, the suitability of a section corresponded to the comparative numbers of grayling seen spawning in the same or similar sections the preceding spring.

TABLE 10.—*Lengths, areas, and estimated amount of stream bottoms suitable for spawning by grayling and hybrid trout in Grebe Lake waterways (July 23–25, 1953)*

Waterways	Distance (feet) available to spawners	Total bottom area (square feet)	Grounds suitable for spawning	
			Square feet	Percentage of total area
Tributaries:				
Hatchery Creek and branches	4,030	19,727	15,053	76.3
South Creek	678	3,965	2,870	72.4
Creek 2	1,000	2,767	552	19.9
Northwest Creek	3,154	18,206	12,578	69.1
Outlet:				
Gibbon River (Wolf Lake to Grebe Lake)	8,106	93,938	42,845	45.6

Time and Water Conditions

The spawning season for both grayling and hybrid trout in Grebe Lake in 1953 and 1954 was between mid-May and late June (fig. 11). Daily average water temperatures during this interval ranged from 40° to 57° F. (tables 11 and 12). The temperatures mid-lake and just beneath the

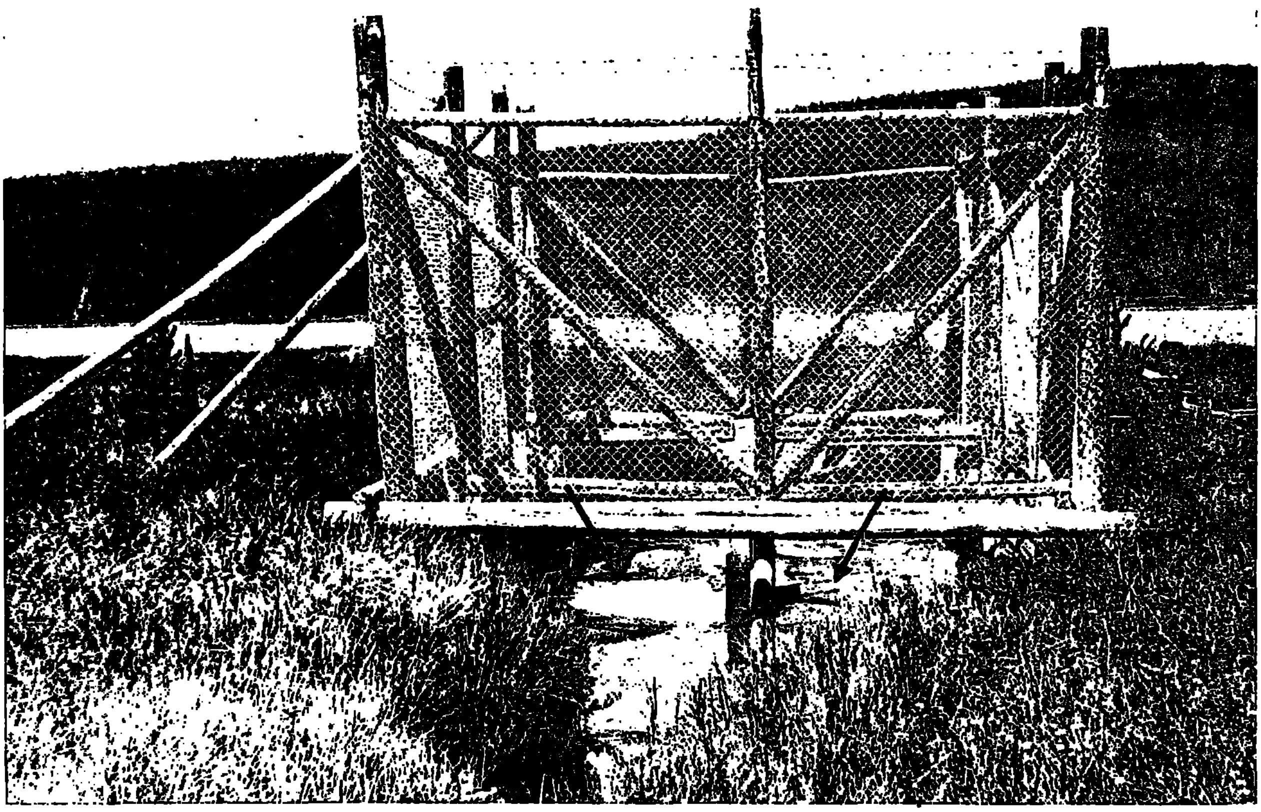


FIGURE 8.—Hatchery Creek trap (with wire-mesh superstructure to keep out bears) in August 1952 after iron rack was removed (at arrows) and fish were allowed access, looking westerly downstream with Grebe Lake in distance.

surface at this time were much like those of the streams.

Within the foregoing extremes there were behavioral differences within and between the two kinds of fishes in the lake (fig. 11). The trout did not have the definite peak of spawning migration (as reflected by movements into traps) that the grayling attained. In most streams spawning travel started 1 to 3 weeks earlier for the trout than for the grayling (tables 11 and 12), and continued at a more or less steady rate throughout the spring over the entire temperature span given above. The range of daily averages was from 40° F. to 50° F. when the grayling runs were heaviest. Temperatures near the surface of Grebe Lake were above 45° F. each year when grayling migrations were maximal (fig. 11).

Spawning Populations of Grayling and Hybrid Trout

There were 10 to 20 times more grayling than trout ascending the spawning streams in 1953 and 1954 (table 13). The actual grayling-trout ratios were 10.5 to 1 (1953) and 19.5 to 1 (1954). The difference in ratios in the 2 years might have resulted from comparing an incomplete count (possibly selective) in 1953, with a relatively complete one in 1954. In the later year, blockades on Northwest Creek, Creek 2, and South Creek seemed to have forced many spawners to accept either the outlet or Hatchery Creek as their spawning site. This may have resulted in larger counts on these two streams than would otherwise have occurred.

Records of spawntakers enumerating weir captures in years previous to 1953 showed that few

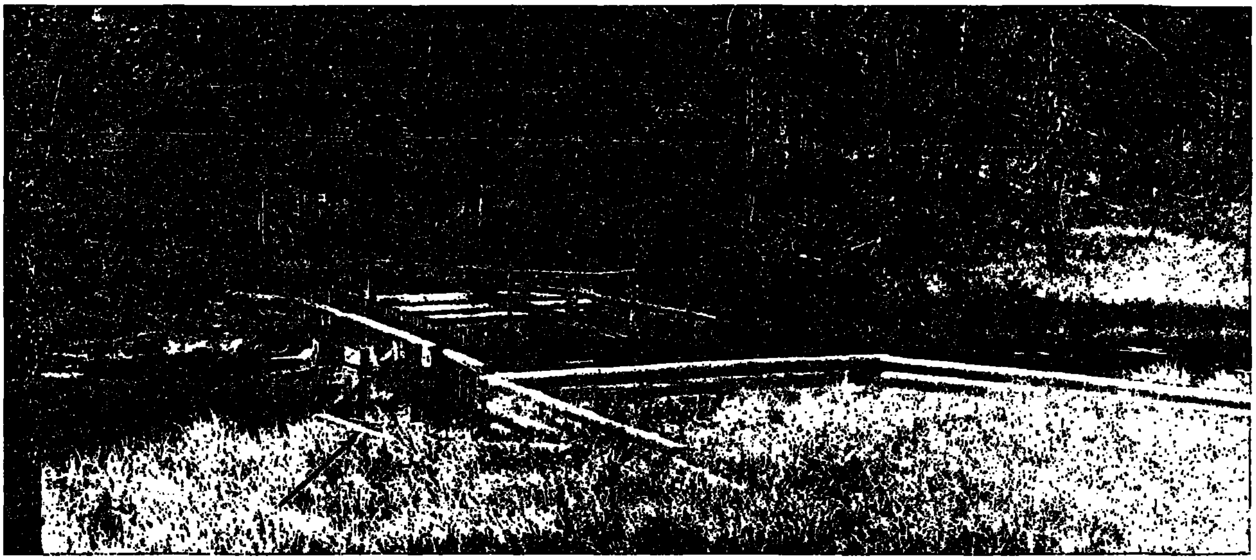


FIGURE 9.—Trap in Gibbon River outlet of Grebe Lake, showing downstream collecting pen (at arrow) July 7, 1954.

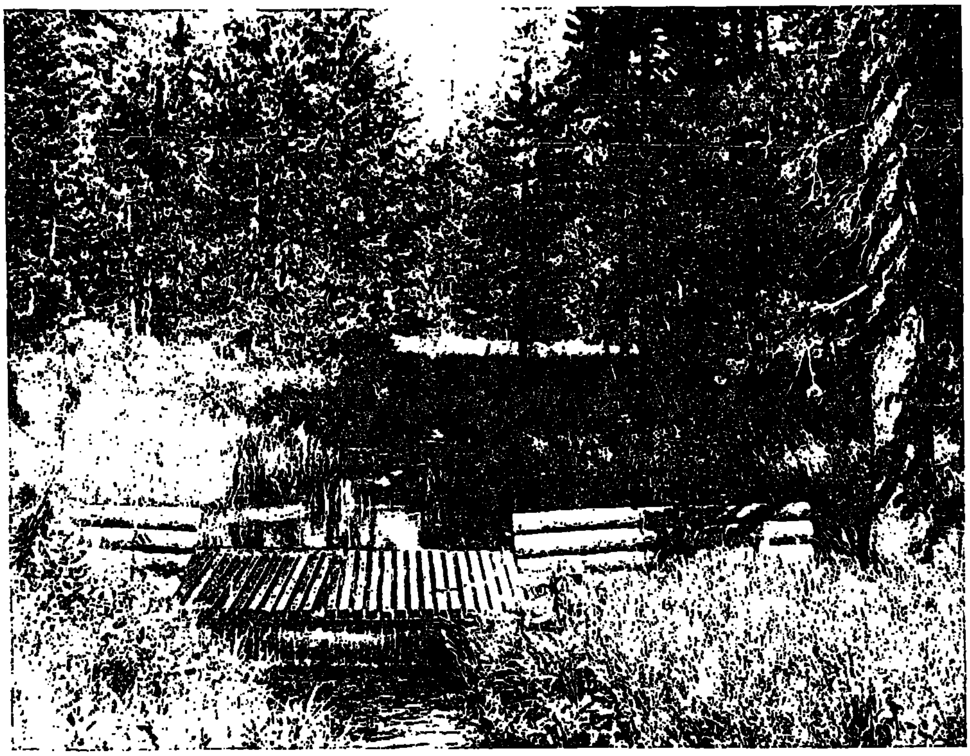


FIGURE 10.—Blockade on Northwest Creek during 1954. The picture was taken in July after the streamflow had dropped.

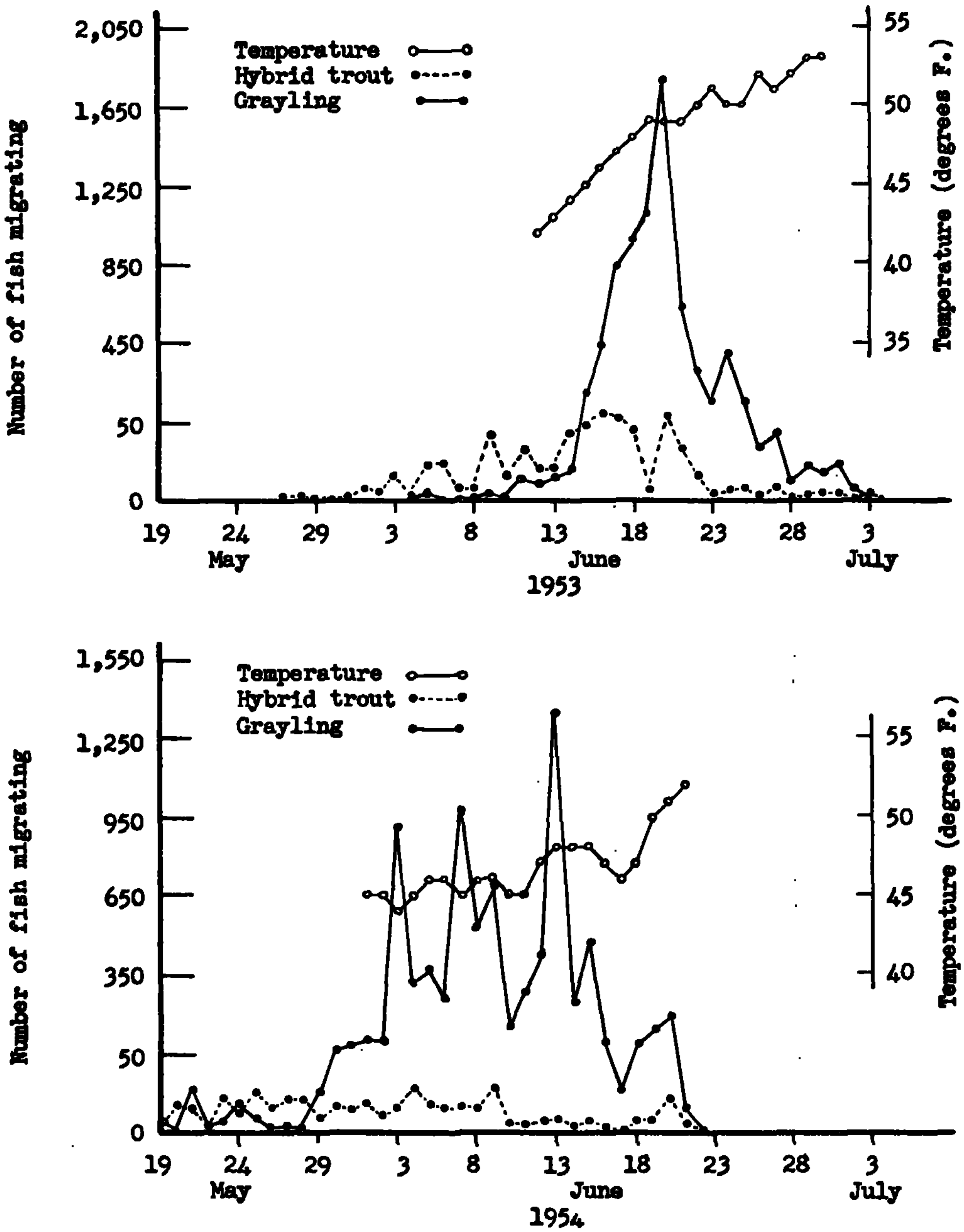


FIGURE 11.—Migration of hybrid trout and grayling into stream traps, and surface water temperatures (6-ft. depth in 1953, and 1 ft. deep in 1954) in Grebe Lake streams, 1953, 1954. Numbers of fish include only those moving to spawning grounds.

TABLE 11.—*Chronology of spawning runs and average daily water temperatures (° F.) for the Grebe Lake stream system (1953)*

Species	Movements [1]	Locations, date, temperature					
		Hatchery Creek	Creek 2	Northwest Creek	South Creek	Outlet	
						Upstream	Downstream
Grayling	First fish	June 14 (46°)	June 17 (43°)	Unknown	June 17	June 5 (36°)	June 8 (39°)
	Maximum activity	June 20 (44°)	June 24 (43°)	----------	June 21	June 18 (50°)	June 19 (50°)
	Last fish	June 26 (45°)	July 2 (47°)	----------	June 24	July 3 (36°)	June 26 (60°)
Trout	First fish	June 6 (38°)	June 1 (37°)	----------	None	June 1 (36°)	May 27 (38°)
	Last fish	June 20 (44°)	July 3 (47°)	----------	----------	July 1 (57°)	June 25 (53°)

[1] Movements recorded were upstream only in the creeks, but both directions in the outlet, as indicated.

TABLE 12.—*Chronology of spawning runs and average daily water temperatures (° F.) for Grebe Lake (1954)*

Species	Movements [1]	Locations, date, temperature					
		Hatchery Creek	Creek 2	Northwest Creek	South Creek	Outlet	
						Upstream	Downstream
Grayling	First fish	May 25 (42°)	None	June 5	June 4	May 19 (40°)	May 19 (40°)
	Maximum activity	June 3 (41°)	----------	June 13	June 12	May 21 (43°)	June 2 (45°)
		June 7 (39°)	----------	----------	----------	----------	----------
		June 13 (42°)	----------	----------	----------	----------	----------
	Last fish	June 21 (46°)	----------	June 21	June 20	June 19 (48°)	June 15 (47°)
Trout	First fish	May 24 (43°)	May 26	May 27	None	May 21 (41°)	May 19 (40°)
	Last fish	June 20 (45°)	June 21	June 21	----------	June 11 (46°)	June 21 (55°)

[1] Movements recorded were upstream only in the creeks, but both directions in the outlet, as indicated.

TABLE 13.—*Comparison of spawning migrants based on weir counts made in 1953 and 1954, Grebe Lake system*

Year and species	Weir counts								
	Outlet downstream migrants	Upstream migrants							
		Outlet	Creek 2	Hatchery Creek	Northwest Creek	South Creek	Total counted	Estimated total	Ratio grayling to trout
1953									
Grayling	263	392	403	5,416	169	438	7,081	10,984	----------
Trout	183	374	97	18	2	----------	674	960	----------
Total	446	766	500	5,434	171	438	7,755	11,944	10:5:1
1954									
Grayling	658	82	----------	5,971	754	413	7,878	7,878	----------
Trout	143	78	34	105	45	----------	405	405	----------
Total	801	160	34	6,076	799	413	8,283	8,283	19.5:1

trout spawned in Grebe Lake tributaries. However, these observations were limited to fish entering the Hatchery Creek weir. In 1953, only 18 of the 5,434 fish which entered this particular trap were hybrids. Spawning trout were relatively more numerous than this in other waterways, but no two streams gave identical indexes of relative abundance of the two species. In the outlet, the Gibbon River between Grebe and Wolf Lakes, hybrid trout comprised 41 percent (183 individuals) of the population migrating downstream in 1953 and 18 percent (143 specimens) in 1954 (table 13). Approximately 50 percent of the fish coming upstream each year were trout;

these were individuals moving toward Grebe Lake, ostensibly to spawn in its tributaries.

From the weir counts it may be concluded that: (1) currently far more grayling than trout use Grebe Lake tributaries for spawning; (2) in tributaries, competition between species for spawning facilities seems minimal; (3) the Gibbon River between Grebe and Wolf Lakes is used by trout and grayling in about equal numbers and is thus perhaps a site of active competition for reproductive locations; (4) grayling-to-trout ratios based on weir counts for any single tributary are not indicative of proportions of spawners of the two kinds in Grebe Lake.

Length frequencies

Length-frequency data were taken on samples of adult grayling trapped in both the 1953 and the 1954 seasons. Polygons of the 1953 data have two distinct modes in the female segment of spawners, and one in the male. In the 1954 material, three peaks are evident for males and two for females (fig. 12). These crests could reflect different age groups in the population. However, growth of grayling in the Grebe Lake watershed was so small in later life that age assessment was essentially impossible (see age-and-growth, p. 333).

Female grayling dominated the sizes below 11.4 inches (total length) in 1953 and below 12.2 inches in 1954. This differential size distribution of males and females is attributable to faster growth in males than in females (as reported for the grayling in Norway, Huitfeldt-Kaas, 1927).

Hybrid trout lengths were much more variable than those of the grayling. Although trout length-frequency polygons show peaks (fig. 13), the numbers of trout comprising each group were so few that the modes expressed cannot be considered as reliable indicators of modal lengths of successive age-groups. Unlike the grayling (where males grew faster than females) female hybrids were of a greater average length than males (fig. 13).

Sex ratios

The potential egg production of a system depends on the number of female spawners as well as upon their individual capabilities. Grayling in the blockaded streams were enumerated by sex as they were passed over the barriers. The males were separated from the females on the basis of the enlarged, sharply pointed, dorsal fin that reached almost to the adipose fin. This fin in the females is smaller and rounded dorsocaudally.

During the early part of the spawning season each year, males of the grayling outnumbered females in the traps on tributaries. As the runs progressed, sex ratios assumed a more nearly 1:1 ratio and ended that way. Combined data from 1953 showed 10 females for every 24 males that entered Hatchery Creek trap (table 14). That overall proportions may change from year to year is suggested by the fact that the ratio of all grayling trapped in Hatchery Creek in 1954 was inverse: 10 females to 7 males. This may have been due to an actual decrease in relative numbers of male grayling in Grebe Lake between the two seasons.

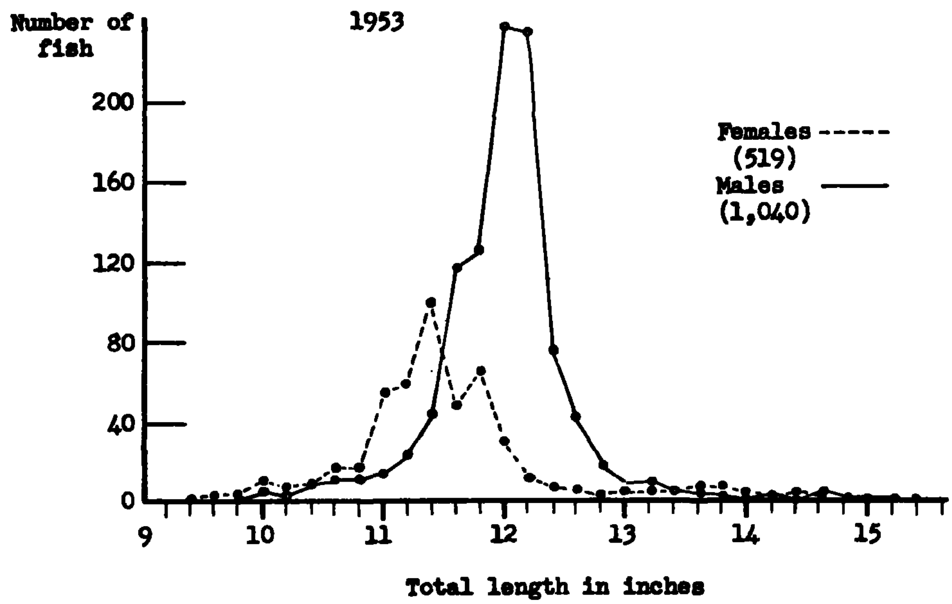
TABLE 14.—*Ratios of females to males (and sample size) for spawning migrants of the grayling in the Grebe Lake system*

Date	Upstream migrants				Downstream migrants	Combined total
	Hatchery Creek	Northwest Creek	South Creek	Outlet	Outlet	
1953	1:2.4 (1,322)	----------	----------	1:0.7 (151)	1:1.3 (87)	1:2.0 (1,460)
1954	1:0.7 (3,634)	1:1.3 (754)	1:1.1 (413)	1:0.6 (83)	1:0.9 (669)	1:0.9 (5,553)

Gustafson (1949) found a 1:1 ratio (93 females to 92 males) among 186 grayling trapped during spawning migrations from Lake Storsjö in Jämtland, Sweden. Ward (1951) reported only 1 female to 3 males on the Cold Creek (Athabaska drainage, Alberta, Canada) spawning grounds but a ratio of 5.1 females per male at the time he trapped fish for spawntaking purposes.

Correct identification of the sexes in the hybrid trout depended upon the observable presence of eggs or milt. Of 234 ripe trout captured in 1953, 80 were females and 154 were males (ratio 1:1.9). In 1954, 141 females and 164 males were identified (ratio 1:1.2).

For the grayling, age on attainment of sexual maturity was at least 3 years. In the hybrid trout, it was 2 years in the males, and 3 in females (see age-and-growth, p. 334).



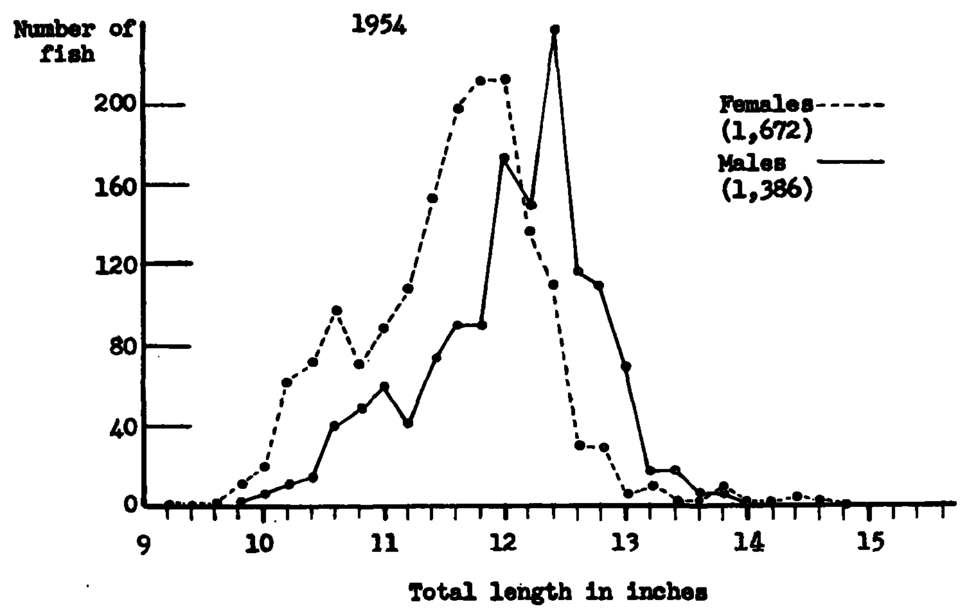


FIGURE 12.—Length-frequency diagram of Grebe Lake grayling captured during the 1953 and 1954 spawning migrations.

Breeding

Male grayling established territories on reaching suitable spawning grounds. Such areas were defended vigorously against other males. The territory varied in size with the extent of the bottom available in that immediate region. In Northwest Creek, males had territories approximately 6 inches wide and 2 feet long. In the outlet where the stream is about 8 to 10 feet wide, they were as large as 4 feet square, or approximately one-half the width of the stream at that point.

Water depth did not seem to be important in site

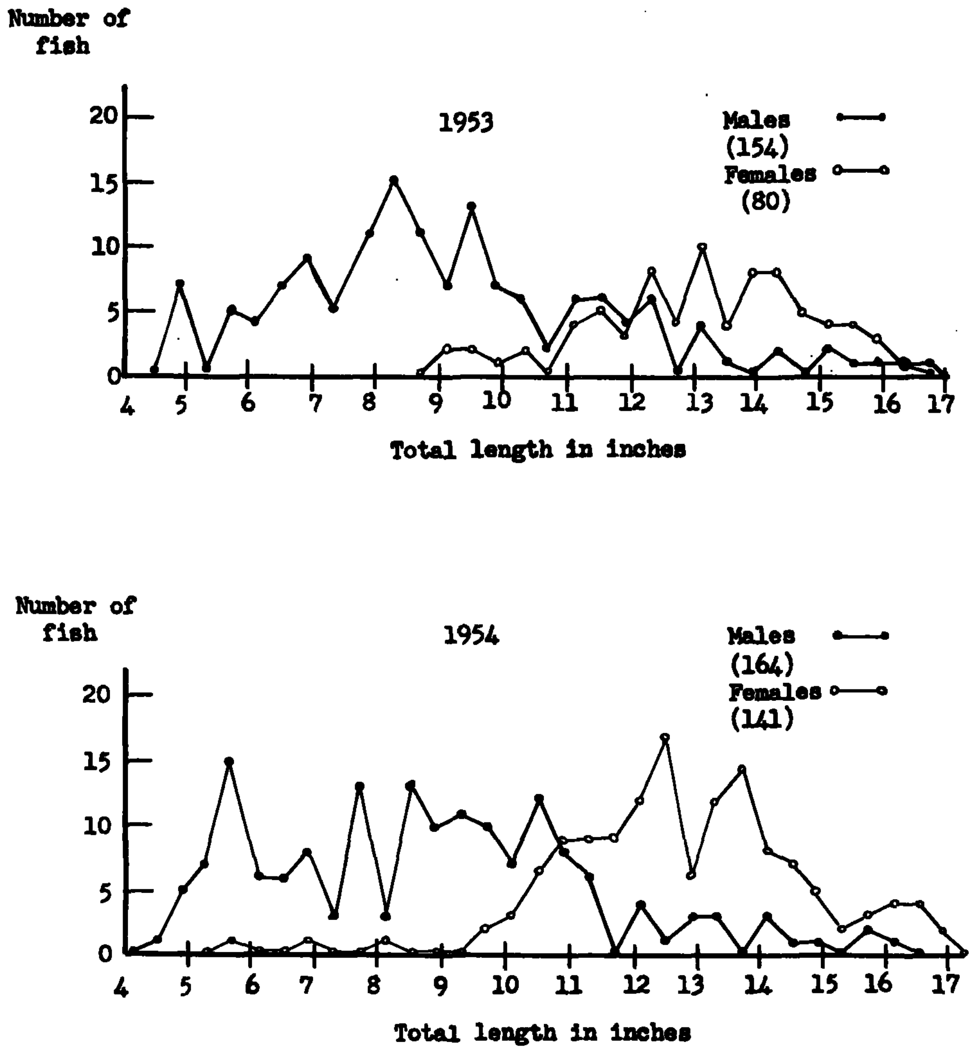


FIGURE 13.—Length-frequency diagrams of Grebe Lake hybrid trout captured during the 1953 and 1954 spawning migrations.

selection by males. Some were in water so shallow that their backs and those of the females were out of water while spawning. Tryon (1947) published a picture of a grayling on its spawning location in water so shallow its dorsal fin was emerging from the water. Other territories used for spawning were in the Gibbon River between 4 and 5 feet deep. Because of the large number of spawning fish, nearly every available location was preempted by males.

Fish on the spawning grounds became uneasy at sudden movements and shadows, but within a matter of minutes returned to spawning activities. Brown (1938) also observed that spawning grayling, though wary, were without apparent fear.

When fighting in defense of a spawning site, the mouth of the guardian male was open slightly so that the white lining inside the jaw could be seen. The dorsal fin was erect and the fish usually threatened the intruder with slightly rigid body movements, then, attacked him. After a few such passes by the aggressive guardian, the intruder would leave the area with the victor in close pursuit. Some unwanted fish were chased as far as 15 feet, after which the defending male would return to the particular part of his territory where he consistently lay.

Often two or three grayling of mixed sexes congregated below a spawning pair and appeared to be consuming eggs that drifted downstream before settling to the bottom. On one occasion a drift net (described later, figs. 17 and 18) was set below an area (approximately 40 ft. long by 15 ft. wide) in the outlet in which several males and a few females were spawning. Three pairs of fish spawned from 3 to 40 feet above the net while it was in position. The current velocity was about 3 feet per second. Only 6 eggs were recovered by the net (4 dead and 2 fertile) and these could have been eggs from a previous spawning which were dislodged from the bottom by the spawners. Brown (1938b) also failed to collect eggs in a screen placed directly behind spawning grayling. One male and one female grayling were examined from those spawning in this area. The male's stomach contained no eggs, only caddis cases and amphipods. The female had recently swallowed a single egg and was full of dipteran larvae.

The grayling in Sweden (Fabricius and Gustafson, 1955) is mostly polygamous. Three females under observation spawned 19, 27, and 34 times, respectively, in 1 day, the first 2 with 2 different males; the third was with only a single male. The daily peak of spawning activity of these Swedish grayling was in the afternoon. Males left their territories about midnight and did not start returning until between 9 and 11 a. m. Grayling were seen spawning in Grebe Lake tributaries at all hours of the day, but no observations were made at night.

Males attempted to spawn with all females entering their territories and sometimes with other males. No females were seen to be attacked (as was noted by Fabricius and Gustafson, 1955). However, if the female was not ready to spawn, she kept moving away, and took refuge under a bank or among other fish. Often the male followed for as much as 8 feet, exhibiting courtship behavior. The male drifted repeatedly toward the female, inclining his dorsal side (particularly his extended dorsal fin) toward her. When the female was ready to spawn, the male moved closely against her to fold his dorsal fin over her back. The male then vibrated his entire body while maintaining a rigid form. The female, after 1 or 2 seconds, began to shiver. The two fish with backs arched, headed into the current, and with mouths gaping, sank to the bottom. A cloud of silt and gravel was swept upward as the vibrating caudal fins came near the bottom; eggs and milt were extruded at this time. Grayling eggs are adhesive and when first released stick to the particles that are stirred up, and also adhere to the bottom. Fabricius and Gustafson (1955) found that in *Thymallus thymallus* the male also bends his tail across that of the female. The female of *T. thymallus* curves her body and with vigorous vibrating movements works her genital opening deep into the gravel before extruding her eggs.

Brown (1938b) observed one female that spawned twice within 45 minutes (each time with a different male). He suggested that the egg laying interval lasts from 2 to 4 days per individual. I found that females placed within fenced enclosures appeared to have completely spawned on the fifth day. After completion of spawning, the grayling moved back into Grebe Lake or Wolf Lake.

Mortality

To investigate distribution of fish and natural mortality, many spawning-run individuals were marked and released in 1953 and returns sought in 1954. In 1953, plastic streamer tags were placed on 142 grayling (artificially spawned the preceding day). These fish were then released below Hatchery Creek trap. In addition, 153 individuals were similarly tagged and placed above the trap to spawn naturally. Of the 295 grayling tagged during 1953, 62 were recovered during the 1954 spawning migrations. Nineteen of these had lost their tags. Of the 43 returns still carrying their tags, 23 belonged to the naturally spawned group and 20 to the group that had been artificially spawned. It would appear that artificial spawn-taking incurred no greater mortality than natural reproduction.

Both during 1953 and 1954, fish migrating into streams other than Hatchery Creek were fin-clipped distinctively in each waterway, not only to avoid counting individuals twice, but also to identify further movements (table 15). In the outlet, fish traveling upstream (into Grebe Lake) had their right pectoral fins removed. The adipose was clipped from downstream migrants. During the 1953 population study, 1,032 grayling were further distinctively fin-clipped (left pectoral) and released.

Spawners marked in 1953 tended to return to the streams in which they had been marked the previous year, but some straying occurred (table 15).

TABLE 15.—*Number and place of fish marking in 1953, and 1954 recaptures*

Type of mark and place of release (1953)	Species	Number marked and released	Locations and numbers of recoveries (1954)						
			Outlet		Creek 2	Hatchery Creek	North-west Creek	South Creek	Total
			Up-stream	Down-stream					
Adipose fin removed	Trout	183		6		1			7
Outlet downstream	Grayling	263	1	30		3			34
Right pectoral fin removed	Trout	374	8	19	1	4	1		33
Outlet upstream	Grayling	392	1	51		44	4	1	101
Left pectoral fin removed	Trout	295	1	5	2	3	1		12
Lake	Grayling	1,032	1	13		117	6	8	145
Streamer tags	Trout	7							
Hatchery Creek	Grayling	295		1		55	2	4	62

EGG PRODUCTION, DEVELOPMENT, AND HATCHING

Perhaps the most fundamental of all factors controlling populations is the annual recruitment to the breeding stock. The greatest mortality is suffered before, during, and immediately after hatching. To obtain an insight into the amount of mortality in the Grebe Lake system during these early stages of fish life it was necessary to develop experimental procedures for estimating egg production and fry returns to Grebe Lake.

Fecundity of Grebe Lake Grayling and Trout

A knowledge of potential egg production in spawning was prerequisite to later estimates of fry yield. Eggs were taken from 37 spawning grayling and counted. These 37 fish were in three total-length groups; (1) less than 11 inches, (2) between 11 and 12 inches, and (3) 12 inches and longer. The average number of eggs of females, respectively, in the foregoing length groups were: 1,889, 2,344, and 2,781 (table 16).

These values are not greatly unlike those found by other investigators. Brown (1938*b*) stated that grayling trapped at Grebe Lake in 1935 averaged 1,650 eggs per female. One 12-ounce specimen (approximately 14.5 inches total length) contained 5,563 eggs. Brown (1938*b*) also found 3 females in Georgetown Lake which averaged 32 ounces and contained 12,946, 12,642, and 8,135 eggs, respectively. Rawson (1950) reported most of the females used for spawn-taking at Reindeer Lake, Alberta, Canada, in 1948 and 1949 produced from 4,000 to 7,000 eggs apiece with a few of the largest containing more than 10,000 eggs per female.

In order to estimate potential and total egg production, females of the grayling spawning in streams were grouped in the same length intervals as above. The potential egg production for the different inlets and the outlet were computed for the 2 years (tables 17 and 18). The results showed an approximate total egg potential of 8,640,000 in 1953 and 10,600,000 in 1954.

TABLE 16.—*Number of eggs per female (based on 37 specimens of the Grebe Lake grayling 1953, 1954) by total length groupings*

Size of fish (inches)	Average size	Mean number of eggs	Range	Standard deviation	Confidence limits 95 percent	
					Upper	Lower
Below 10.95	10.5 [1] (11)	1,889	1,348–2,166	328.8	2,110	1,668
10.95 to 11.95	11.5 (13)	2,344	1,307–2,928	503.6	2,648	2,040
11.95 and over	12.4 (13)	2,781	1,836–4,166	855.8	3,298	2,264
Combined	11.5 (37)	2,362	1,307–4,166	700.6	2,596	2,128

[1] Parentheses contain number of fish in each group.

TABLE 17.—*Potential grayling egg production on various Grebe Lake waterways in 1953*

Number of females and expected egg production	Waterway					
	Outlet		Creek 2	Hatchery Creek	North-west Creek	South Creek
	Up-stream	Down-stream				
Number of spawning females	350	143	192	1,677	1,127	146
Expected number of eggs	831,754	339,830	456,276	3,985,290	2,678,248	346,960
Maximum number (upper 95 percent limit)	950,488	388,342	521,411	4,554,195	3,060,571	396,489
Minimum number (lower 95 percent limit)	713,020	291,320	391,142	3,416,384	2,295,924	297,431

NOTE.—Total expected number 8,638,358; maximum, 9,871,496; minimum, 7,405,221.

TABLE 18.—*Potential grayling egg production on various Grebe Lake waterways in 1954*

Number of females and expected egg production	Waterway: Outlet, Up-stream	Waterway: Outlet, Down-stream	Creek 2	Hatchery Creek	North-west Creek	South Creek
Number of spawning females	51	346		3,512	429	201
Expected number of eggs	122,481	830,947		8,434,349	1,030,278	482,718
Maximum number (upper 95 percent limit)	140,831	955,444		9,698,037	1,184,641	555,041
Minimum number (lower 95 percent limit)	104,130	706,449		7,170,661	875,915	410,394

NOTE.—Total expected number 10,900,773; maximum, 12,533,944; minimum, 9,267,549.

Fewer hybrid trout were collected for egg counts than grayling. The average number of eggs for each of 10 female trout (average size 12.2 inches total length; range 9.0 inches to 14.8 inches) was approximately 780 eggs (actual count). Potential egg production was derived for the entire system each year (table 19). This expected number of hybrid eggs was about 257,000 in 1953, and 143,000 in 1954.

Egg-Development and Hatching

Eggs of the grayling become fully water hardened at 24 hours and measure 3.74 to 3.85 millimeters in diameter. Hatching starts on day 16 and is completed by day 21 at an average water temperature of 51° F. (range 46°–61° F.) (Watling and Brown, 1955). At Grebe Lake, the earliest hatching is about June 25 in the outlet and the latest, about August 9 on the rest of the tributaries except South Creek (latest hatching date observed on South Creek was July 23). Although females spawn approximately in a 1½-month period, most of the eggs hatch and the fry drift into Grebe Lake within a 10-day period. Thus fry from early spawning adults apparently have little growth advantage over the fry of late-spawning adults.

TABLE 19.—*Potential trout egg production in Grebe Lake 1953–54*

Year	Approximate number of female spawners	Number of eggs per female [1]	Egg production: Expected	Egg production: Maximum	Egg production: Minimum
1953	331	775±216	256,525	328,021	185,029
1954	184	775±216	142,600	182,344	102,856

[1] Based on 10 females (average total length 12.2 inches; range 9.0 to 14.8 inches). The range of the number of eggs per female was 335–1,294.

Determination of Natural Hatching Mortality

In the Grebe Lake system two methods were used to appraise the efficiency of natural spawning of grayling in producing fry. One was by the use of traps to collect all possible fry of a known number of grayling and the other was by setting drift nets in tributaries at intervals during the time of downstream migration of newly hatched fish.

Above the intake dam for the fish cultural station, Hatchery Creek is repeatedly and naturally divided. The many individual tributaries of its system have permanent sources in springs or are of temporary derivation from melting snow. The dam at the station effectively blocks fish from further upstream migration into the tributaries above it. Although ascent may be possible during high water of some spring seasons, no adult fish were observed above the dam.

The mainstream of Hatchery Creek, 300 yards above the dam, is approximately 2½ feet wide and ½ foot deep during July and August. Since this stream is spring-fed, the temperature remains low and fairly constant in these months with mean daily values approximating 47 degrees F. One section of this creek, about 70 feet long, was separated from the remainder by ½-inch hardware cloth screens at its upper and lower ends. The bottom within this enclosure was composed largely of gravel and rubble up to 6 inches in greatest dimension. The current varied with a maximum of about 2 feet per second. Where trash accumulated along the screening at the lower barrier, a shallow pool 1 foot long and 1 foot deep was formed.

Fifty yards downstream from the lower barrier a fry trap of the inclined-plane type (Wolf 1951) was installed (fig. 14). The trap consisted of a board dam from the top of which a screen trough slanted down to the holding pen or pot below the dam. The slant of the trough was adjusted so that most of the water filtered through the screen. The overflow carrying the fry dropped into the holding pen. Screen for the entire unit (plane, trough, and pen) was 12 meshes per inch.

On June 22, 1953, five ripe female grayling and five ripe males were placed in the fenced section of the stream. The average size of the females was 11.3 inches (range, 10.4 to 12.0 ins.) and that of the males 12.0 inches (range, 11.2 to 12.3 ins.). When these fish were removed two weeks later (July 2), apparently all had spawned. The

FIGURE 14.—Inclined-plane fry trap used in Hatchery Creek, July 1954.

abdomens of the female fish were flabby and no eggs could be stripped from them. On June 29, the fry trap had been installed.

Fish first appeared in the trap on July 7, ten days after its installation. Three trout (less than 3 inches in length) entered the trap between July 7 and July 26. Grayling fry first appeared on July 25, about a month after the eggs had been spawned. A total of 177 grayling fry and three hybrid fingerlings were counted in the interval from July 7 to August 9. On August 18 electric shocks failed to yield any additional fish. The number of eggs contained by the five females stocked in the enclosure was estimated (method in table 16) to have been $11{,}247 \pm 1{,}567$ and the mortality was $11{,}070 \pm 1{,}567$, approximately 98 percent.

The previous experiment was repeated in 1954 with minor differences. The mesh size of the screen plane, trough, and pot was finer (14 per inch) and the trap was installed immediately after the spawners were placed in the fenced section. Lengths of the five females were from 10.4 to 12.1 inches and averaged 11.8 inches. The five males ranged from 11.2 to 13.2 inches in length and averaged 12.1 inches. The ripe adults were placed in the area on June 18, and removed June 23.

As a result of having the fry trap installed simultaneously with the adults, a measure of egg loss was obtained. The first eggs appeared in the pot on June 19, and the last drifted down into it on July 3. A total of 829 eggs accrued. This represented 6.8 percent of the estimated number of 12,139 eggs in the five females (based on table 16).

The first fry, three in number, entered the trap July 20. Small fish continued appearing until August 6, but only 505 fry (4.2 percent of the estimated potential number) drifted into the trap. Percentagewise this was twice that of the previous year, and probably resulted from the greater efficiency of the 14-mesh-per-inch screen used in 1954, rather than from the different chronology of events.

All of South Creek was utilized for a similar study in 1954. On June 4, 201 females of the grayling and 212 males were placed above the blockade. The fish were removed 2 weeks later. Below the blockade a dam was built to raise the water level and a Wolf-type trap was installed (fig. 15) similar to the one on Hatchery Creek.

The first fry appeared in the trapping basket July 5, and although they continued to come until July 28 most of the young had entered the trap by July 15 (fig. 16). This weir was removed August 3, when no fish could be seen in the creek. A total of 11,404 fry were actually counted. The number of eggs liberated by the 201 spawning females was approximated at $482{,}718 \pm 72{,}323$. The fry returned represented approximately 2.4 percent survival of the expected number of eggs, quite in line with the other two experiments of smaller scale.

A similar survival study with hybrid trout indicated that trout hatch much later in Grebe Lake streams than do the grayling. Although 16 female trout were used for egg production, only 12 small trout fry had been recovered by August 30 when the experiment was terminated. Some cutthroat trout in Yellowstone Lake overwinter in small tributaries (Laakso and Cope, 1956) and such an occurrence may also be common for

FIGURE 15.—The South Creek fry trap and the method of counting young fish.

Grebe Lake hybrids. Vibert-type containers (Vibert 1950) were used in Hatchery Creek for comparing development times between grayling and trout. It was found that all grayling eggs had hatched by the 19th day of incubation, but the last trout fry did not appear until the 37th day (water temperatures 39.0° F. to 48.4° F.).

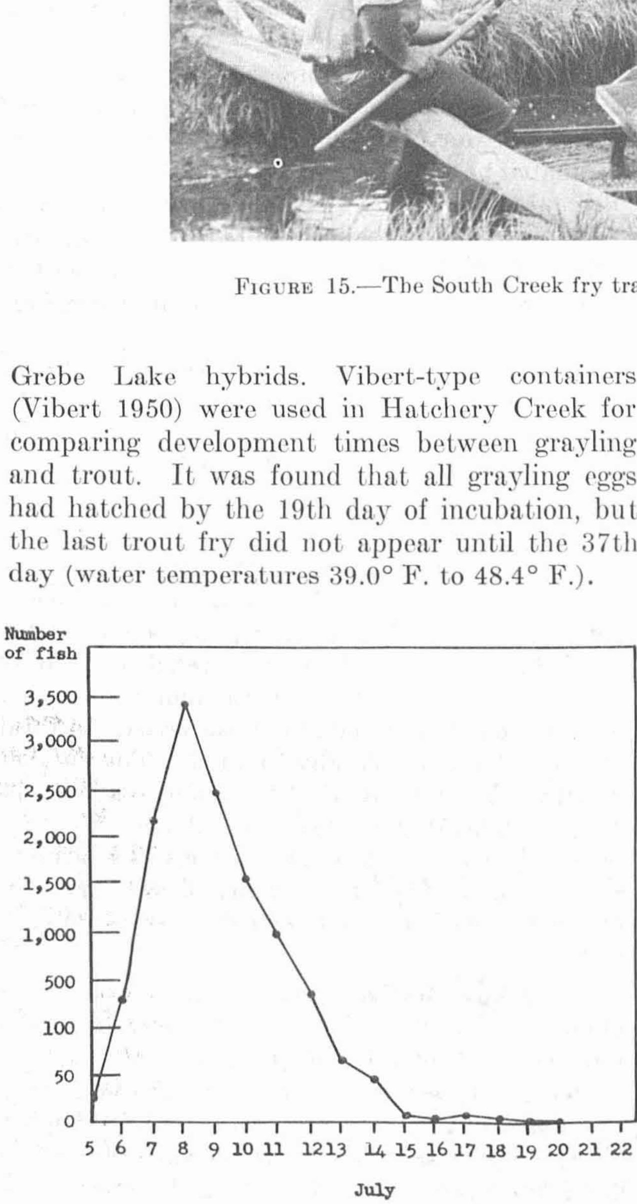


FIGURE 16.—Daily movement of fry downstream into South Creek fry trap, July 1954.

Since it was impossible to measure the actual fry production on all creeks, a method of estimation was devised utilizing drift nets. Each net was built on a rectangular frame made of ¼-inch iron rod, 2 feet wide and 1 foot high. To this frame was attached a bag of bobbinet nylon (26-mesh-per-inch), sewn to the iron rod by a strip of tent canvas (figs. 17, 18). The nylon bag was 6 feet in length to enable exhaust of large volumes of water. In Northwest Creek the following method of capturing fry with these nets was used. A board 1 by 12 by 36 inches was notched just smaller than the drift net frame opening. A ledge of wood below the notch supported the frame when it was in place. This board was placed in the creek to function as a dam. It was sealed with a sheet of canvas and both the dam and canvas were held in place with gravel. All of the streamflow ran over the notch into the nylon bag. The net itself was further supported by a rope from a stake on shore to a snap on the upper edge of the frame. Two 24-hour periods of sampling were employed. The net was placed in the stream for a 15-minute interval and removed for 30 minutes while the counts were made. The time of greatest fry movement occurred between 7:30 p. m. and 10:30 p. m. (fig. 19). Fish that hatched during the daylight hours could be seen accumulating in little

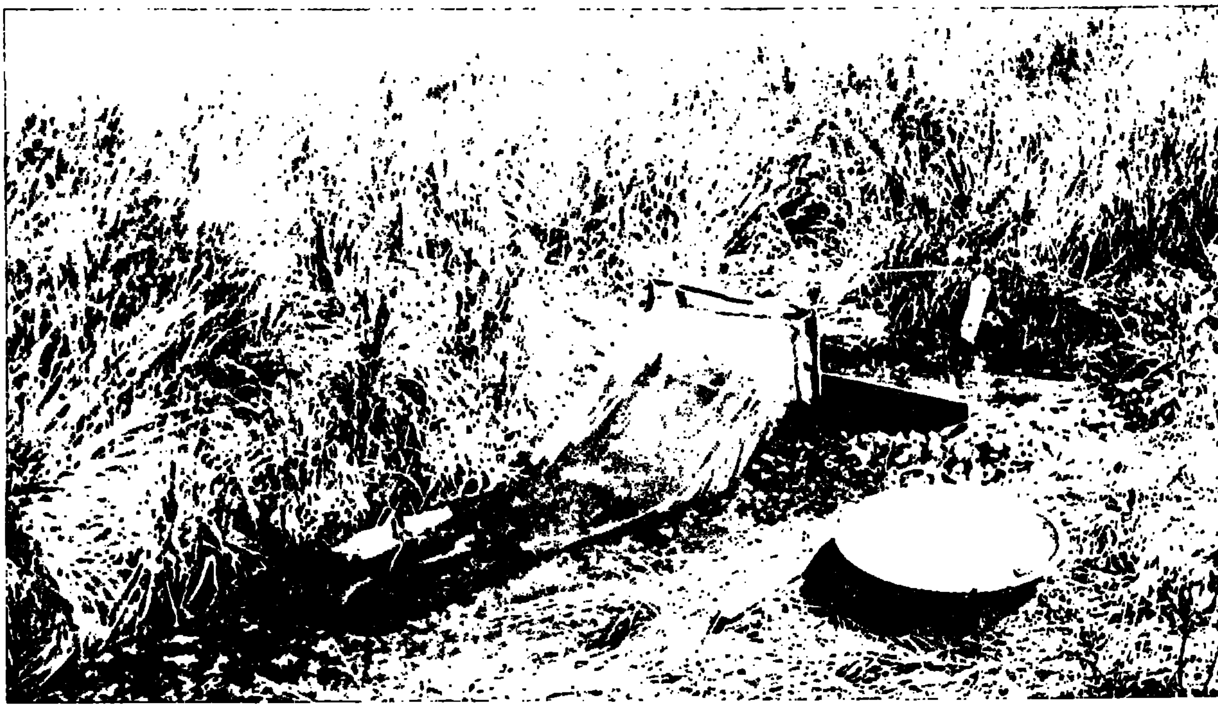


FIGURE 17.—Drift net used on Northwest Creek July 1954 looking upstream.

FIGURE 18.—View looking downstream into drift net and board dam on Northwest Creek, 1954.

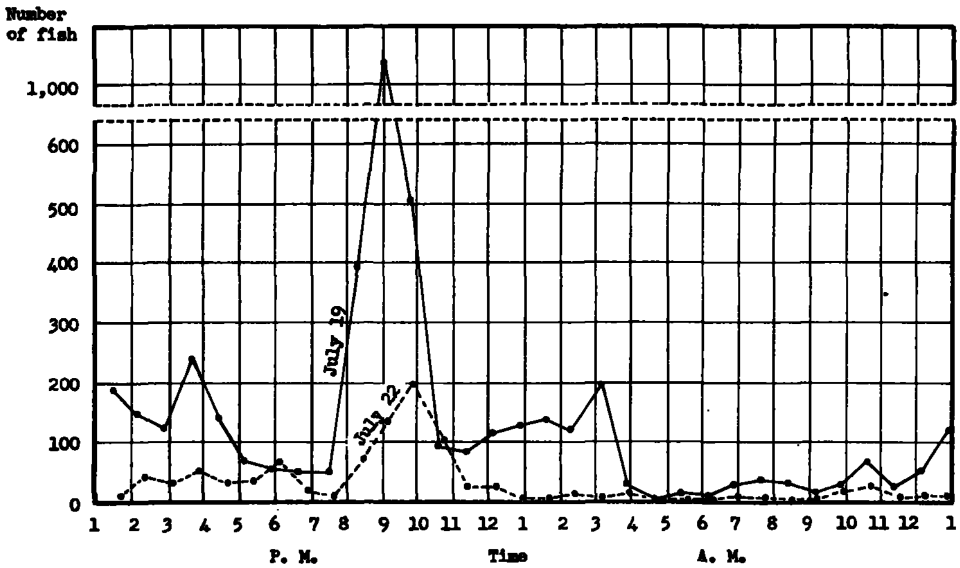


FIGURE 19.—Movement of fry into Grebe Lake over a 24-hour period as reflected by drift net captures on Northwest Creek, July 19, 22, 1954. Each dot represents a 15-minute collecting period.

quiet-water coves and in eddies along shore. These fry moved to faster water about dark, drifted downstream and entered the nets in large numbers until 10:30 p. m. Consequently, from 7:00 to 9:00 p. m. was used daily for sampling the fry production. The percentage of a day's expected total capture that would be expected between 7:00 and 9:00 p. m. was calculated from the 24-hour sets. The daily 2-hour tabulations were then expanded into total daily figures and the results combined to give an approximation of total fry production in the stream.

From the results it was estimated that 58,893 fry entered the lake from Northwest Creek in 1954. A total of 329 females and 425 males had been counted upstream. It was visually estimated that 100 more females spawned below the barricade. This total of 429 females would have an egg potential of $1,030,278 \pm 154,362$. The estimated number of fry represented a return of 5.7 percent (upper limit 6.7 percent; lower 5.0 percent). Although this approximation is higher than counts on other areas where all fry were captured, grayling were not confined to a particular section as in Hatchery Creek and had more spawning area available per individual than on South Creek.

The natural fry production of grayling in the Grebe Lake system in 1954 (table 20) may be approximated from the several sources available in these data as 236,448. The estimated return to the lake by Hatchery Creek is based on the 2.362-percent return found in South Creek. That for the other tributaries is founded on fry movement studies in them.

In the literature, no direct comparisons on mortality of the grayling in early life history stages in North America were available. Gustafson (1949) in his study of the grayling in Sweden captured 0.26 percent of the fry from the estimated total number of eggs laid in a stream during the spawning season. However, he reported that some grayling stayed in these streams for 4 summers, so this did not represent the true survival from eggs to fingerlings.

Foerster (1938), from three tests of natural propagation, found 1.13, 1.05, and 3.23 percent survival of sockeye salmon from estimated egg deposition to the seaward migrating smolt stage. Brasch (1949) in Wisconsin reported an 80 percent survival in five brook trout redds. Hobbs (1948) in New Zealand found a 59 percent to 87 percent survival to fry of all eggs deposited by brown trout.

The real causes of the high mortality of naturally spawned grayling eggs could not be identified with certainty. Nevertheless some possible explanations are discussed below. They lead to the conclusion that the greatest losses are due to egg dislodgment and subsequent current transport of eggs from the spawning beds.

TABLE 20.—*Spawning populations and estimated fry return to Grebe Lake of grayling in 1954*

Grayling	Hatchery[1] Creek	Northwest Creek	South Creek	Total
Female spawners	3,512	429	201	4,142
Estimated fry production	166,151	58,593	11,404	236,448

[1] Estimated fry production for Hatchery Creek based on 2.362 percent return in South Creek and expected number of eggs released by spawning females minus the 1,400,000 removed by fish cultural activities.

Low efficiency in fertilization.—Several authors have commented on the small amount of milt produced by males of the grayling (Brown 1938b; Rawson 1950). However, in nature the efficiency of fertilization seems high. In 59 naturally spawned eggs from Alberta, Canada, Ward (1951) found only two that were unfertilized. In the Grebe Lake hatchery, fertilization, as measured by fry hatch, is usually more than 90 percent.

Egg predation.—Predation on eggs often reduces the numbers available for hatching in fishes but does not seem to be important in the Grebe Lake system as shown by food studies by me, or Brown (1938a). I recovered only 37 eggs from stomachs of 13 female grayling, and none from 4 trout captured on the spawning grounds. Brown (1938a) found 137 eggs in two Grebe Lake grayling taken from spawning weirs and 35 eggs in two fish of six that he sampled in Agnes Lake, Mont. Eggs eaten at spawning apparently represent a "cleaning-up" of those that drift downstream and would therefore be lost to production. I have never observed a grayling engaged in rooting eggs on the spawning grounds.

Dislodgment of eggs during incubation.—A factor in the mortality of eggs is movement after they have been laid on the spawning grounds. Both reproductive activities of the grayling itself and environmental forces are accountable. In areas, such as the tributaries of Grebe Lake, where many adults are crowded for reproduction, it is inevitable that spawnings occur repeatedly over the same sections of stream bottom. After water hardening, eggs are not adhesive and, when dislodged by subsequent spawners, are swept downstream. Some of the embryos may be killed by water turbulence and others by sharp contact with the bottom. Still others may be deposited by the current in habitats unsuitable for development. I witnessed dislodgment many times, and Nelson (1954) found evidence of it in the eggs that he collected from pools where the grayling had not spawned. In my experiment on Hatchery Creek, 829 eggs (of a possible 12,139) drifted into the fry collecting basket. That some of these eggs were dislodged by factors other than spawning activity was shown by the fact that 125 of them entered the basket after the adult fish had been removed from the enclosure. Obviously these eggs had become separated from the substratum through agencies other than the action of adults. However, there was no observable movement after the second week of the 5-week collecting period. Slight changes in water level and current velocity seem accountable for part of the displacement which occurred.

AGE AND GROWTH OF GREBE LAKE FISHES

A knowledge of the age composition of the fish population as it relates to sexual maturity, legal size limits, and growth rates in other areas was obtained by taking scales from Grebe Lake fishes.

Scales from hybrid trout and grayling were collected in 1952, 1953, and 1954. A subsample of 15 fish in each 1½-inch size group was utilized in 1952 and 1953. In 1954, five male and five female grayling in each one-half-inch size interval were collected and used. All trout scales obtained were utilized in age and growth studies.

For use on a microprojector, imprints of grayling scales were made in plastic (0.02 inches thick) by use of a roller press. These plastic impressions were supplemented by water mounts and glycerin-gelatin slides of some scales of grayling older than age-group III when it became necessary to observe whether or not growth had been added in the posterior margin of the scale. Trout scales were cleaned and mounted on glass slides in a glycerin-gelatin medium.

For calculation of growth histories, trout scales (magnification 82.7) were measured from the focus to the anterior margin along an imaginary line bisecting the scale (fig. 20). Average scale lengths for each age group were calculated for each previous year of life. These average scale readings were then converted into average fish lengths by the formula:

Fish length at annulus $X=$

$$\frac{(\text{Total fish length}-\text{k})\,(\text{Scale radius to annulus})}{\text{Total scale radius}}+k$$

The constant (k) is a correction factor derived from the scale-body relation. In 1953 the value of

FIGURE 20.—Scale of a 4-year-old hybrid trout (total length 12.7 ins.) captured July 13, 1954, showing terminology used in identifying various regions. Fish did not have scales at the start of its second summer and annulus I is missing.

k was 2.07 and in 1954, 2.40. The procedure of averaging scale measurements follows that suggested by Van Oosten (1953).

Measurements of grayling scales (magnification 41.5) were made from the estimated center of the focus to a ventral scale margin (expressed as if in situ on the fish). Back calculations were made from scale averages using the above formula and a correction factor (k) of 0.86 in 1953 and 1.14 in 1954.

Problems in Age Assessment of Grebe Lake Grayling

Definition and validation of the annulus

The initial problem in age assessment of grayling scales is the definition and validation of the annulus. The interpretation of all of the marks on the scales of grayling collected during 1952, 1953, and 1954 from Grebe Lake was not clear even after a detailed analysis.The following information was developed during the study.

The first and second annuli on grayling scales were formed when growth resumed or accelerated in the spring (figs. 21, 22). A clear hyaline border first formed around the scale and was followed by a shadowy circulus which started near the anterolateral border and developed both in the anterior field and caudally until it was continuous around the margin. This year mark exhibited strong "cutting-over" of the outermost incomplete circuli in the posterolateral corners of the scale.

Annuli later than the first two were preceded in the anterolateral corners by a clear hyaline area and usually by broken circuli along the anterior border of the scale. Posterolaterally such year marks might cross only one or two circuli and were seldom complete in the posterior field after the third annulus.

The time of completion of annulus formation for yearlings was found to be in the third week of June, by the following procedure. In 1954, collections of grayling, which hatched the previous

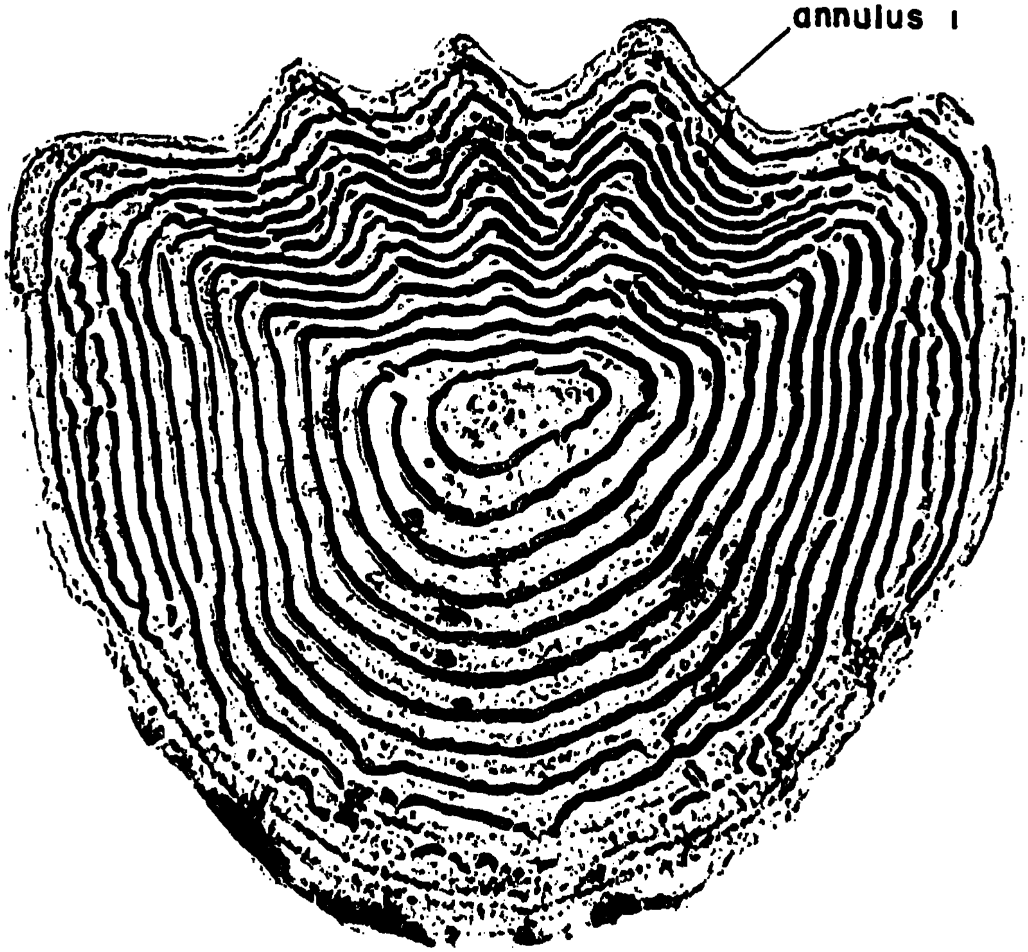


FIGURE 21.—Scale from a 1-year-old grayling (total length 5 ins.) captured June 8, 1954. Annulus has just been completed.

year, were made at intervals throughout the growing season by seining along the shore of the lake after dark. The series was started on May 24, 4 days after the ice disappeared from Grebe Lake. Lake temperatures ranged at this time from 44° F. at the 1-foot level to 41° F. at 25 feet. Hatchery Creek (the main tributary) reached a maximum of 49° F. during the day and a minimum of 34° F. at night. By June 18 when annulus formation was 94 percent complete (table 21), lake temperatures averaged 1° F. higher than each of those given above.

TABLE 21.—*Time of annulus formation in Grebe Lake—grayling entering their second summer*

Sampling date, 1954	Number of specimens	Total length, inches		Percentage with annulus started	Percentage with annulus completed	Number of new circuli beyond annulus	Number without scales [1]
		Mean	Range				
May 24	7	2.36	1.3–4.0	0	0	0	2
May 30–31	7	3.01	1.5–4.1	83	0	0	1
June 8	20	3.28	1.5–5.1	90	15	0–1	0
June 18	19	4.03	2.0–5.2	100	94	1	2
June 26	27	4.18	2.3–5.3	100	100	2–4	2
July 6 [2]	21	4.59	2.8–6.2	100	100	4–5	1
July 18 [2]	21	4.50	3.2–6.2	100	100	7–9	5
Total	122						13

[1] Number without scales at time of annulus formation.
[2] All fish smaller than 3.9 inches were examined. Of these, all specimens from 3.6 inches to 3.9 inches and larger fish randomly chosen had scales developed at time of annulus formation.

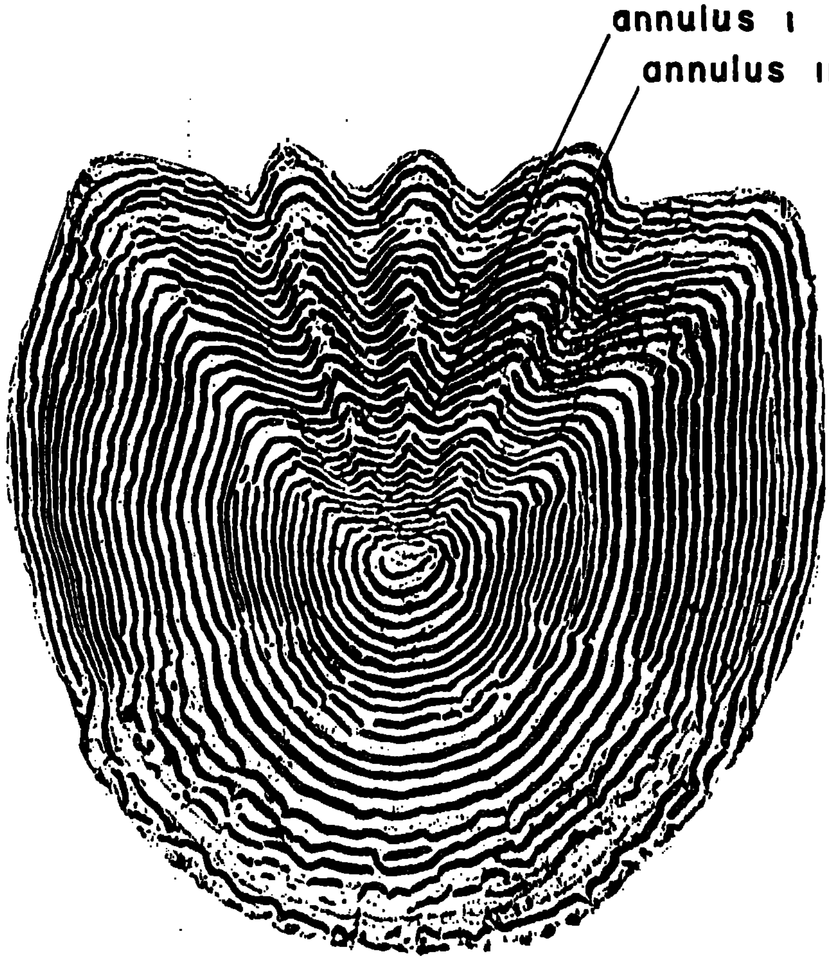


FIGURE 22.—Scale from a 2-year-old grayling (total length 9.2 ins.) captured June 10, 1954. Annulus has been completed for the present year.

Two-year-old grayling averaged very little earlier than yearlings as to time of annulus formation. All thirteen 2-year-olds collected between June 10 and 26, 1954, had a complete annulus for the current year. The first fish taken, June 10, had already added 4 to 6 new circuli beyond the second year mark.

Three-year-old grayling had a different growth pattern from younger ones. The fish of age-group III reported on here were trapped during their first spawning migration. No scales from 3-year-olds less than 13 inches in total length had an evident annulus during the current year. However, some fish longer than 13 inches showed a sub-marginal third-year mark. Consequently, 1 year was added empirically to the age of all fish 3 years old and older, when the expected year mark was not evident at or near the scale margin.

Growth subsequent to the third annulus was small and slow in both body and scale lengths. In age-group III during the remainder of the 1954 season, I found individuals in the last week of July that appeared to have just completed their third annulus. By the end of the first week of August, all specimens clearly of this age-group that were studied had deposited only one to three new circuli beyond the year mark. In years of life after the fourth, growth continued slow or ceased altogether, making further annulus recognition impossible.

Failure of first annulus to appear

A second problem in the age assessment of grayling scales was the apparent failure of annulus I to appear in certain fish and in certain years. The year 1953 was such a year in Grebe Lake.

The late breakup of ice in June 1953, with its associated retarded season, might explain the number of yearlings captured throughout the spring and summer of 1954 (table 21) which were too small to have scales at the time of annulus formation and hence lacked annulus I. The survivors of these small fish would thus occur in later years as a year older than their scale record shows. The scales of such individuals appeared to be recognizable by the great distance from the focus to the first annulus in relation to the pattern on the scales of individuals that became yearlings under conditions favoring "normal" growth and scale formation. In grayling belonging to year-classes previous to 1953 and which started growth during seasons about which I have no information concerning early spring conditions, I assumed 5½ inches to be the maximal amount of growth that could be expected of a grayling in Grebe Lake during the first year of its life. All fish calculated to have attained more than 5½ inches at the end of their first year of life were considered to be without annulus I. The data were adjusted accordingly by adding 1 year to the observed age.

Failure of scale growth and effect on annuli

The third problem of age assessment in grayling scales is that beyond the age of III (sometimes beyond age II) annulus formation is uncertain. As stated, there was little growth after 3 years of age. Furthermore, on some scales there was evident disappearance of parts of previous circuli and annuli after the third winter. Erosion of circuli in grayling has been noted previously by Brown (1943) who stated that such erosion was superficial, not peripheral, and therefore did not influence growth calculations. However, when only one or two circuli were deposited between the third and fourth year marks and erosion occurred, it sometimes became impossible to interpret the correct age of the fish.

Two sets of experimental data demonstrated the age assessment complications resulting from the failure of scale growth and resorption of scale markings in or after the third year of life. One set was from a lot of known-age grayling introduced into Grebe Lake and the other was from returns on individuals captured, scale-sampled, tagged, and released.

In 1949, the small number of grayling spawners led to the planting of 125,000 fry and 100,000 eggs for the first stocking in 3 years. The 1949 year-class appeared strongly in 1952 as 3-year-old fish (90 percent of the sampled population belonged to age-group III). In 1953, fish that dominated the samples had the following characteristics: (1) a strong third annulus, (2) some growth beyond annulus III, and (3) a circulus near the edge of the scale having all the criteria, though weakly, of a true year mark, with a little additional growth beyond. Scales from these grayling could have been assessed in one of two ways: (1) as 5 years old, by assuming the circulus near the margin which crossed one or two other circuli and was continuous through the anterolateral corners was a true annulus, or (2) as 4 years old, by considering the mark just described as a false annulus or a check.

In 1953, 300 grayling were tagged with white plastic streamer tags (see Joeris 1953, for techniques and description) and released in Grebe Lake. Of 43 recaptures made in 1954, 38 had belonged to the age-group with the same scale picture as the fish that dominated the catch in 1953. These fish showed only one or two new circuli and no more annuli than were present the previous year. Thus the grayling tagged in 1953 and recaptured again in 1954 could have again been called 4- or 5-year-olds on the basis of their scale markings. The year's growth of these tagged individuals averaged only 0.3 inch. The circulus near the edge of the scale, which could have been interpreted as an annulus the previous year, often appeared eroded and indefinable in the recaptured fish. The tags themselves may have had a detrimental effect upon these fish as was found with the use of jaw tags on pike (Williams 1955) or trout (Alvord 1954). However, the scale morphometry of untagged grayling in 1953 and 1954 (fig. 23) was so similar to the tagged fish of approximately the same size that correct age assessment for the population older than 3 years remained in doubt. The modes of length-frequency diagrams (if valid as indicative of age-groups) suggest a growth of 0.4 inch between the fourth and fifth years of life for the males of the spawning population (fig. 12); growth in the tagged males averaged only 0.1 inch less. Scale increments related to body increments as small as this do not show growth signs that can be interpreted as annuli. Alvord (1954) found that in 69 brown trout, which added less than 0.8 inch to

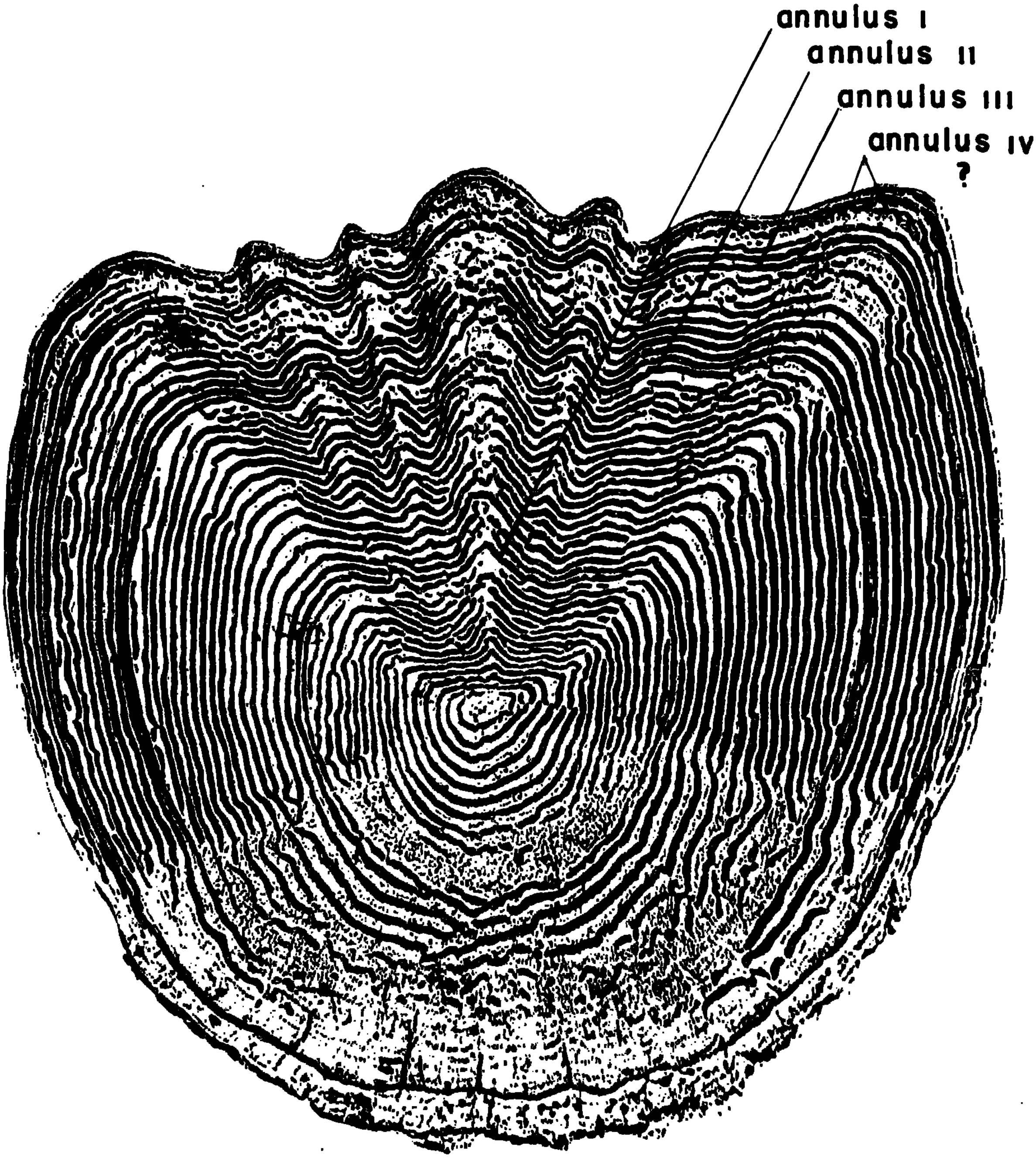


FIGURE 23.—Scale of a grayling of indeterminate age (total length 12.8 ins.) captured May 24, 1954. Fish is starting either its fourth or fifth summer.

total length during 1 year (September to September), 59.4 percent did not form a year mark.

Failure to assess age beyond III was not experienced by Brown (1943), Miller (1946), Nelson (1954), or Creaser and Creaser (1935). However, a scale photograph by Brown (1943) from a previously collected sample of Grebe Lake grayling is suggestive of a problem not unlike one presented by this study.

Growth of Young Grayling

Growth in the first 2 years was determined empirically by measurements of samples taken at intervals through the growing season until September 1, 1954. Plots of average lengths at time of capture and time of season indicated a reasonably rapid and constant growth rate for this first year (fig. 24). Lengths of fish in their second summer (from preserved specimens) were taken from grayling captured at night when the fish moved toward the shoreline and could be seined effectively. These collections, started 4 days after the ice cover had disappeared, showed a continuing trend of growth in the fish, until the 6th of July (fig. 24). The measurements for age-group I might have tended to reflect only the smaller fish, however, since some larger yearlings had moved to deeper water as evidenced by their appearance in trap nets set during the seining period.

Calculated Growth Rates Compared

Growth rates were determined for grayling in the first 3 years by calculating the 1-year-olds and 2-year-olds separately and treating fish 3 years of age and older as a single age-group. Average total fish lengths (inches) to the first three annuli were: I, 4.4; II, 8.9; III, 11.2 (table 22).

In studies of the grayling in North America, length has been measured by different methods. Biologists in Canada (Miller 1946; Rawson 1950) and Alaska (Wojcik 1955) used the fork length measured in millimeters. In the United States, Brown (1943) took standard lengths in millimeters and total lengths in inches. Nelson (1954) and the present study have utilized total length measurements in inches.

To compare rates of growth among different study areas it was necessary to develop relationships between the various types of length measurements. Fork lengths and total lengths were determined for 17 grayling from Alaska and 33 specimens from the United States. All were in alcohol at the University of Michigan Museum of Zoology. In addition, 45 Grebe Lake grayling less than 5.5 inches total length (formalin preserved) were measured. Conversions between total and fork lengths were read directly from a

TABLE 22.—*Average calculated lengths in inches of Grebe Lake grayling for their first 3 years of life in 1953 and 1954 samples*

Date of collection	Year class	Total length at various annuli			Number fish
		I	II	III	
1953	1952	4.4			59
	1951	3.3	8.3		23
	1950 and over	4.5	8.9	11.2	134
Mean		4.4	8.8	11.2	216
1954	1953	4.1			28
	1952	4.6	8.4		24
	1951 and over	4.5	9.0	11.2	98
Mean		4.4	8.9	11.2	150

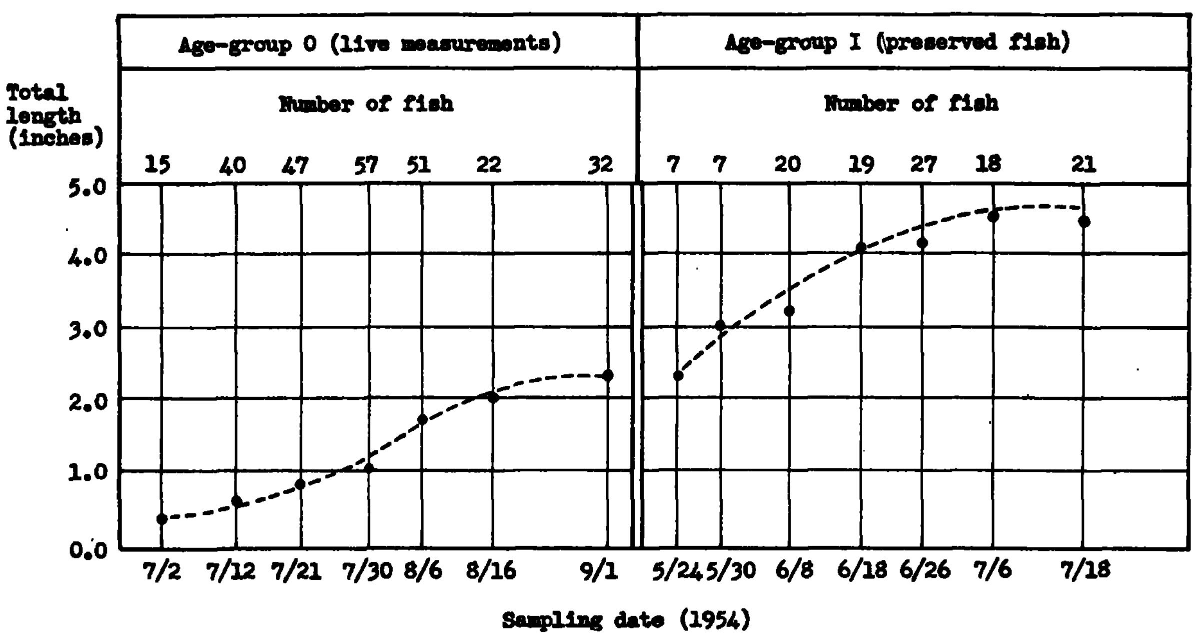


FIGURE 24.—Seasonal growth rates for grayling of age-groups O, I, during 1954.

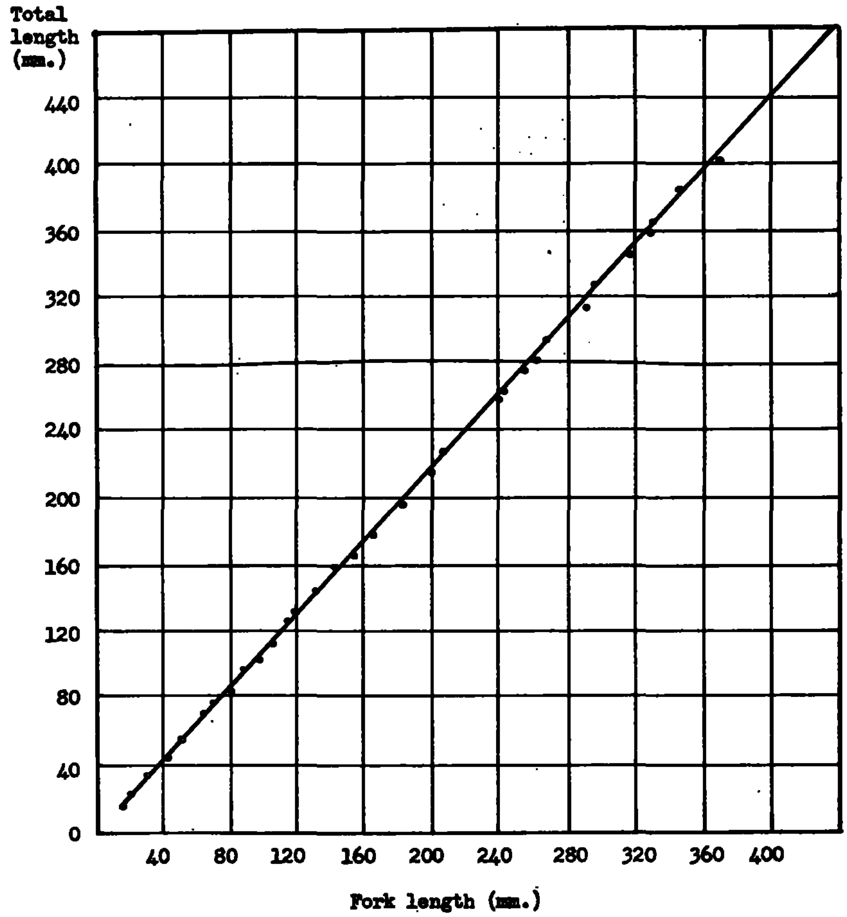


FIGURE 25.—Relation between total lengths and corresponding fork lengths of preserved grayling. Dots represent average lengths in 10 mm. total length intervals. Conversion factors for size intervals are: less than 18 mm., 1.00; from 18 mm. to 22 mm., 1.06; from 22 mm. to 400 mm., 1.097 (figures are for the conversion of fork length to total length).

line of relation of total lengths and fork lengths (fig. 25).

As one proceeds from south to north, the grayling tends to grow more slowly, mature later, live longer, and attain a greater maximum size (fig. 26). The growth of grayling in the Red Rock, Mont., area was fastest during the early years of life. However, beyond age IV the yearly increment became smaller than increments in other areas. The minimum spawning age observed by Nelson (1954) was II; the oldest fish collected belonged to age-group VI.

Grebe Lake grayling grew most nearly like those in Lake Athabaska (figures converted from Miller, 1946). The Grebe Lake fish spawned first at age III. Because of the difficulty in determining annuli beyond III in this body of water, no maximum ages are available.

Although some specimens from Great Bear Lake (Miller 1946) reached maturity during their fourth summer, the majority matured in their fifth. The oldest fish collected belonged to age-group XI.

Males of the grayling (*Thymallus thymallus* L.) in Sweden matured at an age of 2 years and females, at 3 (Gustafson 1949). The oldest individuals found were starting their eighth year of life.

Problems in Assessment of Age in Hybrid Trout

Lack of annulus I

In the trout hybrids, as in the grayling, the first year's growth often appears excessive. Because of this, and because the cutthroat trout in nearby Yellowstone Lake was sometimes without annulus I (Laakso and Cope, 1956), I established two categories of hybrids based on the number of circuli from the focus to the first year mark. In one of these fish, which had more than 15 circuli within this area, an extra annulus was assigned (fig. 20). The first circulus from the focus was used as the first year mark. In the other category, trout with fewer than 15 circuli on the scale between the focus and the first annulus were judged to have their first year mark.

Eroded and broken scales

Many trout scales in 1953 and 1954 had broken edges, clear hyaline spots, and eroded or reabsorbed margins. Such scales were discarded as undependable for age-and-growth analyses. They made up 14.3 percent (22 fish) of the sample in 1953 and 2.5 percent (5 fish) in 1954. Some bias may have been incurred by removing these fish from the sample, because most of the individuals were more than 14 inches in total length.

Age and Growth of Hybrid Trout in Grebe Lake

Averages of calculated total lengths (inches) at various annuli for hybrid trout based on combined samples taken in Grebe Lake, 1953 and 1954, were: I, 3.7; II, 7.2; III, 10.5; IV, 12.8; V, 14.9;

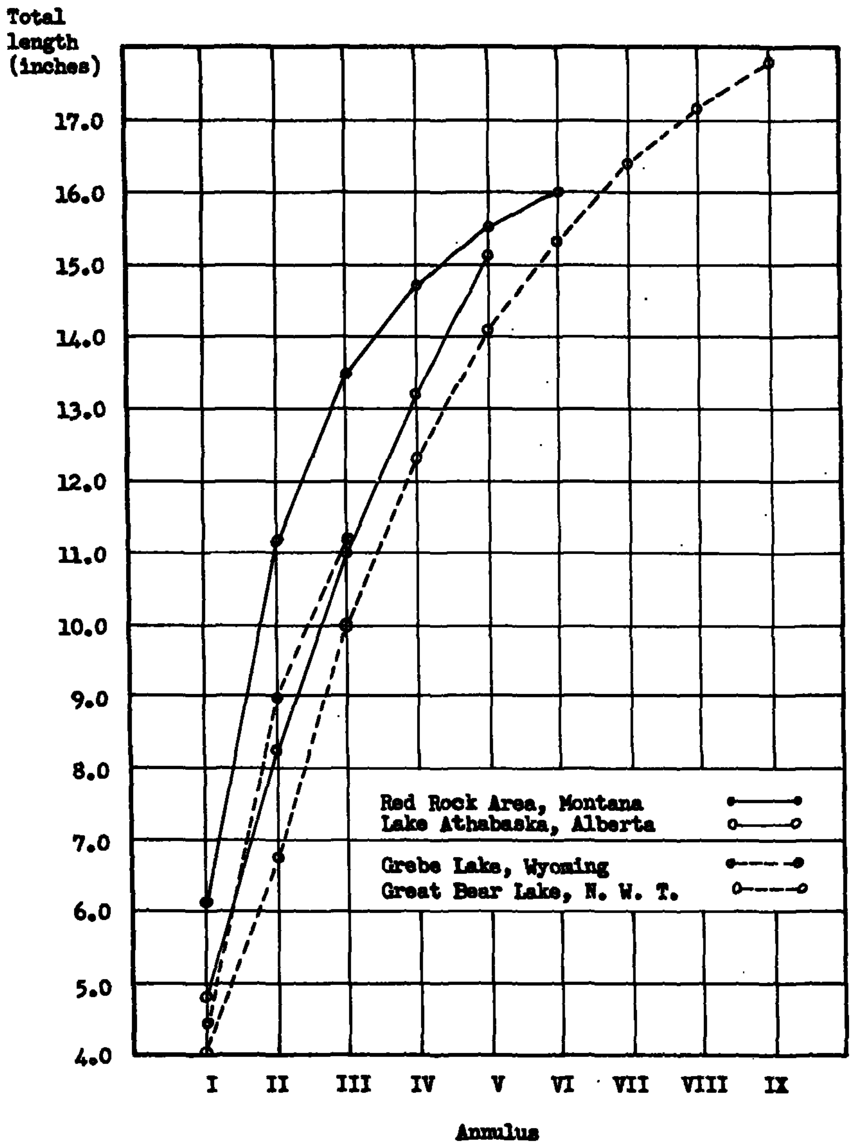


FIGURE 26.—Comparative growth rates of grayling from United States (Nelson 1954, and Kruse, present study) and Canada (Miller 1946). Fork lengths converted to total lengths.

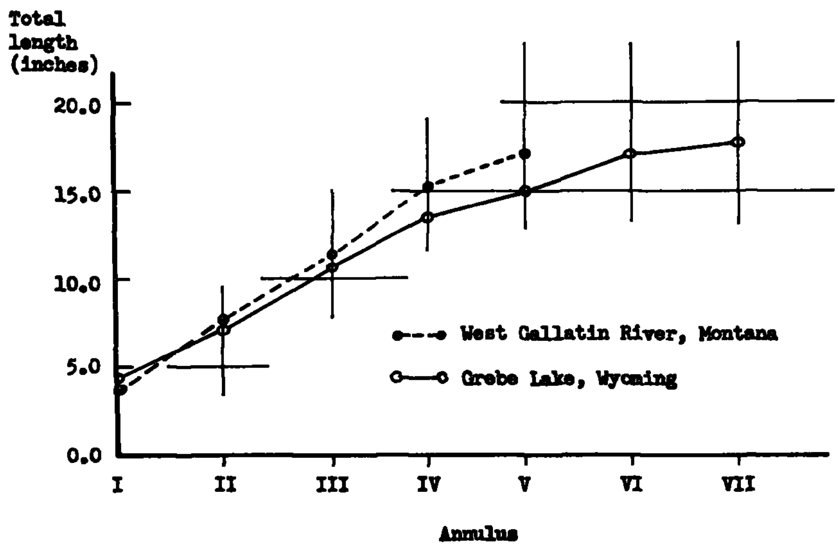


FIGURE 27.—Calculated growth rates of hybrid trout from the West Gallatin River, Mont. (data from three elevations combined, Purkett 1951) and from Grebe Lake, Wyo.

VI, 17.3; VII, 17.5 (tables 23 and 24). This was not maximal. It was slightly less than that in the West Gallatin River through the third year and markedly less than that in the fourth and fifth years (fig. 27).

Some male hybrid trout were mature in Grebe Lake at the start of their third growing season (annulus II). All female hybrids captured during the spawning season were at least 3-year-olds. Trout reached the legal size limit of 6 inches in their second or third year of life.

Female hybrid trout in Grebe Lake grew faster than did the males (table 25), and by the third year females were approximately 1.3 inches longer than the males.

TABLE 23.—*Average calculated total lengths of fish in inches at various annuli of Grebe Lake trout, 1953*

Summer of life	Year class	Calculated total fish lengths at annuli I–VI						Number of fish
		I	II	III	IV	V	VI	
2	1952	3.14						8
3	1951	3.43	6.63					17
4	1950	3.65	7.23	9.97				52
5	1949	3.66	7.41	11.00	12.69			48
6	1948	3.63	6.89	10.86	13.45	15.11		6
7	1947	4.23	8.59	12.57	15.83	16.94	17.60	2
Mean		3.60	7.22	10.53	12.88	15.57	17.60	133

TABLE 24.—*Average calculated total fish lengths in inches at various annuli of Grebe Lake trout, 1954*

Summer of life	Year class	Calculated total fish lengths at annuli I–VII							Number of fish
		I	II	III	IV	V	VI	VII	
2	1953	3.89							4
3	1952	3.99	6.99						38
4	1951	3.81	7.23	10.06					67
5	1950	3.89	7.40	10.90	12.71				61
6	1949	3.63	7.14	10.65	12.64	13.97			22
7	1948	3.88	8.27	13.42	15.39	16.76	18.19		2
8	1947	5.15	8.63	10.78	12.64	14.49	15.98	17.54	2
Mean		3.87	7.25	10.53	12.75	14.22	17.09	17.54	196

TABLE 25.—*Empirical average total lengths of fish in inches in successive years of life for 1953 and 1954 collections of male and female trout in Grebe Lake*

[Number of fish in parentheses]

Sex	Total lengths at year of life				
	2	3	4	5	6
Males	7.2 (32)	9.8 (45)	12.2 (42)	15.3 (1)	
Females		11.1 (30)	13.5 (53)	14.7 (18)	17.9 (4)

Length-Weight Relation

Length-weight relation for both the grayling and the hybrid trout were used in computing pounds of fish in Grebe Lake from length measurements. According to Hile (1936) this relation

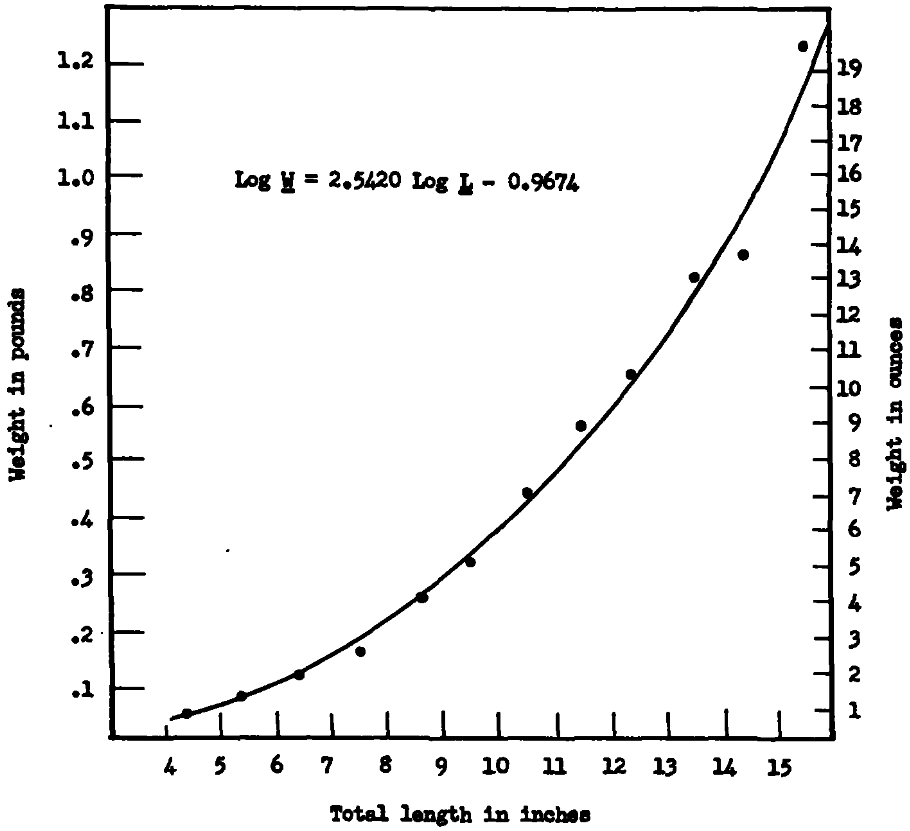


FIGURE 28.—Length-weight relation of 148 hybrid trout from Grebe Lake, Yellowstone National Park. Dots represent average weight within each 1-inch group.

can best be expressed by a parabolic curve of the form $W=cL^n$, where

W=weight of the fish,
L=length of the fish, and
c and n are constants.

Converted to logarithms, the formula becomes, log W=log c+n log L, and the constants can be determined by the method of least squares.

Paired length-weight measurements of 148 hybrid trout were from two groups of individuals. The first group was comprised of fish more than 6.0 inches long and contained both gill-net captures of August 1952, and tagged males taken during spawning runs. The second group was composed of trout under 6.0 inches in length; measurements of these were made on preserved specimens originally seined from Grebe Lake. Since only a limited number of measurements were available for the two species, both sexes were used in calculations (except no length and weights were from spawning females of either species). The 309 grayling used in computations were from gill-net captures (August 1952) (more than 6.3 inches total length) and preserved specimens (less than 6.3 inches).

The calculated curves (figs. 28 and 29) fit the empirical values very well. For the hybrid trout, the predicted weights of fish follow the formula log W=2.5420 log L—0.9674 (fig. 28). In the grayling the length-weight curve is of the form log W=2.7682 log L—1.2925 (fig. 29).

FOOD ANALYSIS

The grayling and the hybrid trout compete for food in Grebe Lake. The extent to which they do this is disclosed in part by a comparison of their stomach contents.

Stomachs were taken from 112 grayling and 24 hybrid trout during 1952 to 1954. These fish were captured with hook and line, by weirs used during the spawning season, and by nets. The stomachs were preserved in 5 percent formalin as soon as possible after collection of the fish. The total content of each was subsequently

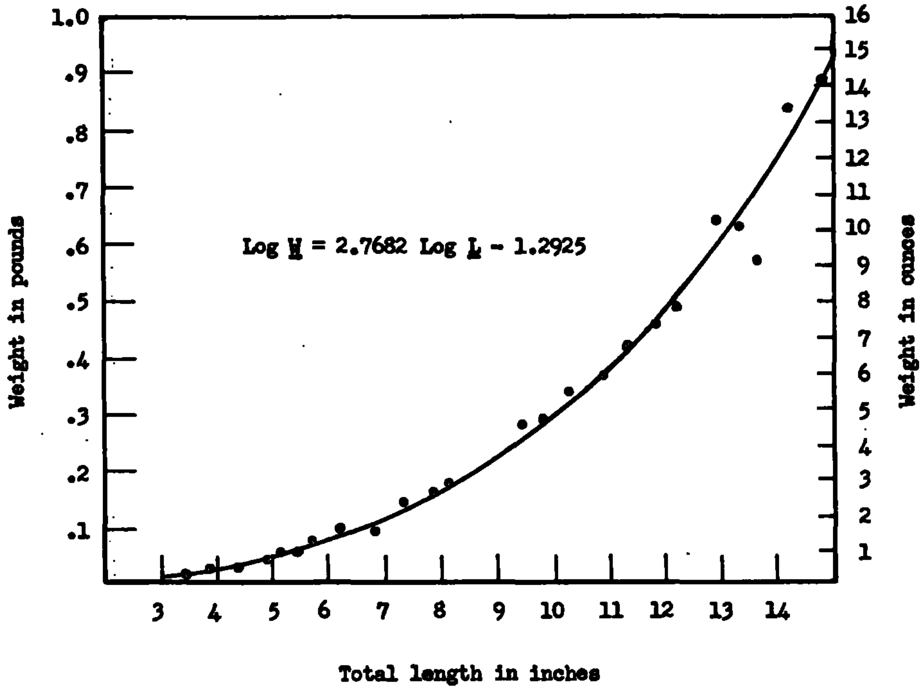


FIGURE 29.—Length-weight relation of 309 grayling from Grebe Lake, Yellowstone National Park. Dots represent unweighted average empirical weight within each ½-inch length group.

measured volumetrically by water displacement. Identifiable organisms were sorted, dried 1 to 2 minutes on blotting paper, and then measured in the same manner as the total contents. However, the small amount of material in trout from the tributaries and in the young-of-the-year grayling precluded such measurement. The organisms most commonly used as food by Grebe Lake fishes follow:

OLIGOCHAETA
- *Lumbricus terrestris*

CRUSTACEA
- Cladocera
  - *Daphnia* (probably *pulex*)
- Copepoda
  - *Cyclops* sp.
- Amphipoda
  - *Gammarus fasciatus*

INSECTA
- Plecoptera (identified by Dr. A. R. Gaufin, University of Utah)
  - *Alloperla* sp.
  - *Isoperla* sp.
  - *Peltoperla* sp.
  - *Nemoura* sp.
- Ephemeroptera (identified by Dr. George F. Edmunds, University of Utah)
  - Baetinae (possibly *Centroptilum*)
  - *Cinygmula* sp.
  - *Rhithrogena* sp.
  - *Baetis* sp. (possibly *intermedius*)
  - *Ephemeralla coloradensis* Dodds
  - *Callibaetis* sp.
  - *Caenis* sp.
  - *Ameletus* sp.
- Odonata (identified by Dr. G. H. Bick, Tulane University)
  - Zygoptera
    - *Ischnura* sp.
    - *Lestes* sp.
    - *Argia* sp.
  - Anisoptera
    - *Cordulia shurtleffi* Scudder
- Trichoptera (identified by Dr. H. H. Ross, Illinois Natural History Survey)
  - *Agrypnia deflata* Milne
  - *Limnephilus* sp.
  - *Mystacides* sp.
  - *Neothremma* sp.
  - *Molanna* sp.
  - *Agapetus* sp.
  - *Rhyacophilus* sp. (identified by Dr. H. C. Chandler, California Department of Fish and Game)
- Coleoptera (identified by Dr. H. C. Chandler)
  - Malachiidae sp.
  - Staphylinidae sp.
  - *Crenitis alticola* (Fall)
- Diptera
  - Tendipedidae (=Chironomidae)
- Hymenoptera
  - Formicidae

TABLE 26.—*Average number of each kind of food organism (and percentage frequency of occurrence) in grayling of age-groups O and I, Grebe Lake, 1954*

Date of capture (1954)	Fish average size (total length in inches)	Number of fish	Food item: Ephemeroptera nymphs	Ephemeroptera adults	Trichoptera larvae	Diptera larvae	Diptera pupae	Diptera adults	Amphipoda	Cladocera	Pisidium	Copepoda	Unidentifiable terrestrial insects
July 2	0.53	5	—	—	—	—	0.2 (20)	—	—	—	—	—	—
July 12	.71	5	0.6 (40)	—	—	8.4 (100)	3.6 (80)	—	—	0.8 (60)	—	—	—
July 21	.87	5	—	—	—	—	—	—	0.2 (20)	13.6 (60)	—	—	—
July 30	1.12	5	—	—	—	—	—	—	—	17.8 (60)	—	—	—
August 6	1.70	5	0.6 (40)	—	—	—	[1] (40)	—	—	[1] 3.0 (40)	—	—	—
August 16	2.08	5	10.6 (80)	0.4 (20)	—	—	—	0.2 (20)	—	—	—	0.2 (20)	—
September 1	2.48	5	[1] 10.6 (100)	—	—	—	—	0.2 (20)	1.0 (20)	20.4 (40)	—	—	—
May 24	2.58	5	1.2 (60)	—	—	27.4 (80)	—	—	2.4 (40)	—	—	—	—
May 30	2.80	5	10.2 (40)	—	—	35.4 (100)	0.2 (20)	—	0.2 (20)	—	—	—	—
June 8	3.74	5	0.8 (60)	—	1.6 (40)	154.4 (100)	11.4 (60)	—	9.4 (60)	—	0.6 (40)	0.4 (40)	—
June 26	4.26	5	0.4 (20)	—	8.6 (100)	15.8 (100)	49.2 (80)	—	2.4 (20)	—	1.2 (60)	—	0.4 (40)
July 18	4.80	5	[1] (50)	—	[1] (50)	[1] (100)	[1] (100)	—	—	[1] (100)	—	—	[1] (40)

[1] Food items in these fish were decomposed and could not be enumerated.

Four principal groups of fishes were sampled for food content: (1) young-of-the-year and 1-year-old grayling collected at intervals throughout 1954; (2) spawning females of grayling and of hybrid trout; (3) small trout (less than 3.4 ins. in length) inhabiting Hatchery Creek during the time the newly hatched grayling fry were descending in July 1953; and, (4) adults of both species taken from the lake proper during the 1952 to 1954 seasons.

Group 1. Grayling belonging to age-groups O and I, collected throughout the 1954 season.—Grayling in this group were taken by seining the shore of Grebe Lake at intervals between July 2 and September 1, 1954. Of all the fish in each collection, only the five that were nearest the mean length in each lot were used in the food analysis.

Young of the grayling start to feed early in life. Some individuals in a group of hatchery-reared fry began ingesting food on their fourth day and by the eighth day all individuals sampled contained food (Brown 1939). The yolk sacs of those that Brown measured averaged 0.3 inches when food was first consumed and had disappeared in most fish by the end of the second week. The smallest specimen that I found with food in it in Grebe Lake (July 2, 1954) had a yolk sac 0.1-inch in length and was probably between 1 and 2 weeks old. In this body of water, young grayling (to 1.5 inches total length) subsisted primarily on *Daphnia* and on Diptera larvae and pupae (table 26), organisms that are especially abundant in the shoal areas of Grebe Lake, which is inhabited by these small fish. Stomachs collected between July 12 and August 6 contained only *Daphnia*. From August 6 to September 1, young fish consumed mainly ephemerids (mostly Callibaetis) along with lesser amounts of Tendipedidae (=Chironomidae) larvae and pupae, *Gammarus*, *Daphnia*, and *Cyclops*. Winged insects (adult Diptera) first appeared in the diets on August 16.

The 1-year-olds collected in the spring and early summer of 1954 had eaten not only a more varied diet, but also were taking larger organisms than were the young-of-the-year. Among the food items were some Trichoptera and relatively more gammarids. The first terrestrial insects were found in stomachs on June 26 from fish averaging 4.3 inches total length. By July 18 the variety of food found in the stomachs of the 1-year-olds was nearly the same as that consumed by older fish (exceptions were the large Odonata of a size too great to be ingested by small fish).

Group 2. Spawning female trout and grayling.—Stomachs of 13 grayling and 5 hybrid trout were obtained from spawning adults collected in the streams tributary to Grebe Lake. Although these fishes readily took food in these streams, very few kinds were available to them and feeding conditions were crowded. Consequently, more than 30 percent (5) of the grayling and 80 percent (4) of the hybrid stomachs were empty. Fish eggs were found in 8 of the 15 grayling sampled (table 27), but the greatest number from any one specimen was only 12. The fact that no sand or gravel accompanied these eggs demonstrated that they had been taken while adrift and not while attached to the substrate.

Group 3. Small trout from tributaries.—Seven small trout were taken with a fine-meshed dip net from Hatchery Creek at the time grayling fry were descending. The smallest of these was 1.8 inches in length and the largest, 3.4 inches (average, 2.3 ins.). These fish contained organisms common to the stream as well as terrestrial insects that had fallen into the water. There was no evidence of cannibalism (table 28).

TABLE 27.—*Food of 13 grayling collected from Grebe Lake tributaries during their spawning season, June 1954*

Food item	Total number	Volumetric composition (Percent)	Frequency of occurrence (Percent)
Plecoptera			
Nymphs	1	2.3	7.7
Ephemeroptera			
Nymphs	2	(1)	15.4
Odonata nymphs			
Zygoptera	20	10.5	7.7
Anisoptera	13	55.8	30.8
Trichoptera			
Larvae	10	12.0	46.2
Diptera			
Larvae	12	(1)	15.4
Pupae	129	7.0	23.1
Hymenoptera	1	(1)	7.7
Fish eggs	37	7.0	61.5
Fish scales	7	(1)	23.1
Food remains		2.3	15.4

[1] Quantity in stomachs too little (less than 0.05 ml.) to be measured volumetrically.

Group 4. Grayling and trout from Grebe Lake proper.—Although competition for food was shown by the contents of the stomachs from 40 grayling and 10 trout captured in May, July, and August, there was no evidence of predation between the two kinds of fishes. Only two grayling stomachs contained scales (table 28). The scales had belonged to two grayling more than 9 inches long and one trout over 8 inches; there was no trace of flesh or bones. Diptera larvae and pupae were the major food items in the group; these were found in 70 percent of the trout and 72.5 percent of the grayling. Fishes captured in Grebe Lake when ice was present (May and June) were subsisting primarily on amphipods and Diptera

TABLE 28.—*Stomach contents of 17 hybrid trout and 40 grayling from the Grebe Lake system, 1952 to 1954*

Food items	Grayling		Trout			
			Creek (7)		Lake (10)	
	Volumetric composition (percent)	Frequency of occurrence (percent)	Volumetric composition (percent)	Frequency of occurrence (percent)	Volumetric composition (percent)	Frequency of occurrence (percent)
Collembola			(1)	14.3		
Plecoptera						
Nymphs		5.0		28.6		
Adults			(1)	14.3		
Ephemeroptera						
Nymphs		5.0		57.1	(1)	20.0
Adults	0.9	10.0	(1)	14.3	1.0	30.0
Odonata nymphs						
Zygoptera	2.4	32.0			1.0	20.0
Anisoptera	3.1	10.0			19.2	10.0
Hemiptera						
Adults		10 0				10.0
Trichoptera						
Larvae	7.9	45.0	(1)	28.6	26.3	50.0
Pupae	1.6	12.5				
Adults	3.6	32.5			4.0	40.0
Coleoptera						
Larvae				28.6		10.0
Adults		12.5	(1)	14.3		
Diptera						
Larvae	5.4	72.5		100.0		10.0
Pupae	2.0	67.5		57.1	1.0	80.0
Adults	1.6	22.5	(1)	14.3	5.6	30.0
Hymenoptera						
Adults	.2	10.0				10.0
Amphipoda	11.2	35.0			17.2	30.0
Cladocera	4.9	42.5				30.0
Nematoda			(1)	14.3		
Aphidae			(1)	14.3		
Pisidium	.3	17.5				
Oligochaeta					2.0	10.0
Trout scales		2.5				
Grayling scales		5.0				
Fish eggs		2.5				
Food remains	53.8	87.5			22.7	70.0

[1] Quantity in stomach too little (less than 0.05 ml.) to be measured volumetrically.

larvae. Later in the season (August) their diet showed greater variety. Some individuals fed primarily on damselfly nymphs, whereas many others consumed mostly adult caddisflies. The major portion of the diet consisted of Trichoptera larvae in the early spring, and Ephemeroptera nymphs in the late spring and summer. Tendipedidae (=Chironomidae) were also taken in great numbers when available.

Previous writers (Brown 1938a; Leonard 1939, 1940; and Rawson 1950) have also found that insects, sometimes aquatic but at other times terrestrial, predominate in the food of adult grayling. Apparently the species feeds on whatever is available and shows no discernible preferences.

Although both the grayling and the hybrid trout in Grebe Lake ingested the same types of food items in approximately equal amounts, there was no apparent antagonism between the two fishes. By way of illustration, during the evening grayling and trout rose to the surface within a few feet of one another with no gross evidence of strife in a common feeding ground. Apparently, there was sufficient food in Grebe Lake for both species, judging from the gorged condition of the digestive tracts and plumpness of the fish. The only exception was on the spawning grounds where many fish were crowded into the small streams; a relatively large number of the stomachs collected were empty.

HARVEST OF GREBE LAKE FISHES BY ANGLING

Despite the recognized limitations of a voluntary creel census it was necessary to employ such a method to obtain information on the magnitude of the sport fishery. The data gave a measure of the effect of angling on the fish population. Also, the reports made it possible to adjust the procedures of the mark-and-recapture population estimate that was in progress. A creel census form was employed to obtain records of the amount of time anglers spent in fishing, the kinds, numbers, and sizes of the fishes caught, whether or not there were identifying marks on the fish, and the types of lures used.

These creel census forms were placed in a box near the parking area, from which all fishermen had to walk the 3.5 miles to Grebe Lake. The importance of completing the creel-census records was stressed by personal contacts with the anglers.

The completeness of the voluntary returns was checked by counts of all fishing parties. In 1953, 65 of 98 groups (66 percent) filled out creel census blanks during the time of the population estimate. In 1954, the response improved slightly; 93 of 132 counted parties (70 percent) completed the forms. For the rest of the seasons in both years it was estimated that only about 50 percent of the fishermen responded.

Adjustment of the creel records on the foregoing basis enabled an approximation of the total catch each year. In the 1953 season, 780 fishermen removed 2,148 fish. Anglers increased to 818 in 1954 and caught 2,863 fish. This represented a harvest of the estimated populations that approximated 7.1 percent in 1953 and 9.9 percent in 1954.

The average size of 81 of the grayling measured from anglers' creels was 11.4 inches. Since this figure was not too different from the 11.0-inch average size of the grayling captured during the population study, I assumed the size distribution of the anglers' catch to approximate that of the trap nets during the respective years. Under these conditions the total weight of fish removed by the fishermen was 903.8 pounds in 1953 and 1,191.3 pounds in 1954.

Although grayling are approximately 10 times as numerous as trout in Grebe Lake, they comprised only 67 percent of the catch in 1953 and 75 percent of the total captures in 1954. Thus in the catch, the grayling-to-trout ratio of 3.1 to 1 in 1954 was higher than in 1953 (1.9 to 1). Personal contact with anglers indicated that most preferred to catch the hybrid trout, and that they fished primarily for it.

Results of creel-census information tabulated by monthly intervals showed a decreasing trend in fish per fisherman between July and September, 1953, but an increase during the same interval in 1954 (table 29). Fishing effort also declined rapidly after August 29 (fig. 30) However, the efficiency of the late season anglers, as reflected by the fish-per-hour rate, increased in September of both years.

TABLE 29.—*Monthly summary of fishing pressure and yield for Grebe Lake, based on 138 creel census returns in 1953, and 140 in 1954*

Item	Date of census							
	1953				1954			
	July	Aug.	Sept.	Total	July	Aug.	Sept.	Total
Number of fishermen	137	200	24	361	206	179	26	411
Number of hours	477	723	56	1,256	601	635	81	1,317
Hours per fisherman	3.5	3.6	2.3	3.5	2.9	3.5	3.1	3.2
Catch:								
Hybrid trout	131	119	12	262	211	128	11	350
Grayling	207	241	44	492	455	537	91	1,083
Unidentified	114	264	5	383				
Total	452	624	61	1,137	666	665	102	1,433
Fish per fisherman	3.3	3.1	2.5	3.1	3.2	3.7	3.9	3.5
Fish per hour	0.95	0.86	1.09	0.91	1.11	1.05	1.26	1.09

The average number of fish per fisherman (3.1 in 1953, 3.5 in 1954) was good considering that the limit imposed by the National Park Service on Grebe Lake was five per angler. Some fishermen who reported limit catches often caught two or three limits and released all but five fish; others released all fish. Only trout and grayling actually removed from the lake were included in the foregoing analysis of yield. Therefore, fishing in Grebe Lake was probably better than the figures indicate. However, there was a compen-

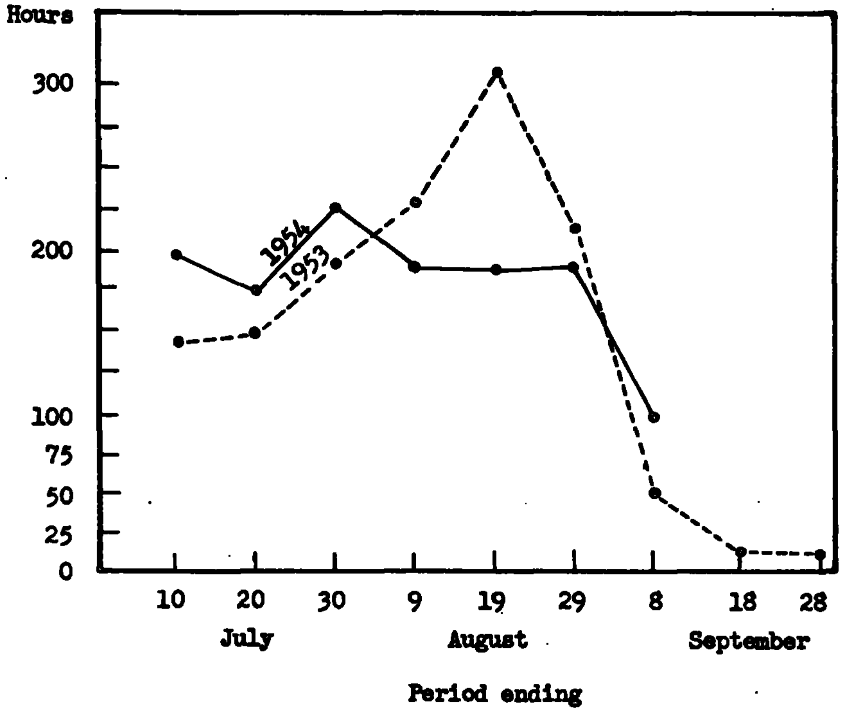


FIGURE 30.—Total number of hours (by 10-day periods) spent on Grebe Lake by fishermen during 1953 and 1954.

satory reaction on the part of fishermen to fill out forms only if they caught fish.

More fish were taken from Grebe Lake by fishermen using flies than by any other method. However, the number of fish taken by any one group of fishermen depended not so much on the type of gear they used as it did on the number of anglers in that group; the percentage of fishermen using any one lure or combination of lures agreed closely with the percentage catch by that respective method (table 30). Since tabulations are not for individual fishermen, but for parties, the combinations occurred where one person in a party would use spinners and another flies, or other lure. The average number of people per party was 2.5 in 1953 and 2.9 in 1954.

Fishing yield from Grebe Lake was low (table 29). There was a harvest of only about 6 pounds per acre in 1953 and 8 pounds per acre in 1954. In contrast, a trout lake in Oregon of similar size and also having a creel limit of five fish produced more than 50 pounds per acre of trout each year between 1945 and 1947 (Holloway 1947). In a series of trout lakes on Grand Mesa in Colorado, anglers were removing an average of 63 pounds per acre per year with two of the lakes yielding an average of 106 pounds per acre per year (Lyall 1941).

PREDATORS AFFECTING GREBE LAKE POPULATIONS

The removal of fish from Grebe Lake by predatory birds and mammals is a factor that affects the size and composition of the population. However, measurement of the effect of predation is difficult. Black bear, *Ursus americanus* Pallas, mink, *Mustela vison* Schreber, and river otter, *Lutra canadensis* Schreber, were seen on Grebe Lake between 1952 and 1954, but they were not numerous, and actual evidence of predatory activities was small. The osprey, *Pandion haliaëtus*, however, took fish throughout each season.

TABLE 30.—*Use of lures and effectiveness on Grebe Lake in 1953 and 1954*

Number of anglers	Catch by various lures						
	Flies	Spinners	Bait	Spinners and flies	Spinners and bait	Flies and bait	Spinners, flies, and bait
Number of parties (total, 305)	152	40	17	59	7	14	16
Percentage use	49.8	13.1	5.6	19.3	2.3	4.6	5.2
Catch	1,412	327	163	499	46	156	180
Percentage catch	50.7	11.7	5.9	17.9	1.7	5.6	6.5

SUMMARY

The grayling, *Thymallus arcticus*, is common both to North America and to eastern Asia. In the United States the species is highly prized by sportsmen because of its great beauty and comparative rarity. The only indigenous population maintaining itself at present in the United States is in the Red Rock Lakes region in Montana. From this center, it was introduced in other waters, including some streams and lakes in Yellowstone National Park, Wyo.

The grayling was first planted in Grebe Lake of the Park in 1921, 14 years after the rainbow trout had been introduced and 9 years after the cutthroat trout had been planted there. The two species of trout intermixed after planting and by 1952 only hybrids were found. The grayling reportedly has experienced wide fluctuations in population abundance at intervals since its introduction. One such decline in numbers in 1949 resulted in the present study on Grebe Lake. The following statements summarize the findings of my work between July 22, 1952, and September 1, 1954.

Grebe Lake is eutrophic with a well-developed thermocline during the period of summer stagnation and a deficiency of oxygen in the deep waters of 1953 and 1954. Samples of the aquatic fauna in Grebe Lake showed a predominance of Tendipedidae (=Chironomidae) both numerically and volumetrically.

Population estimates in 1953 and 1954 were obtained from trap nets and a mark-and-recapture method. About 27,000 grayling were in Grebe Lake in 1953 and 26,000 in 1954. Trout approximated 2,000 the first year and 2,500 the second. The standing crop of fish in Grebe Lake in 1953 was estimated at 77 pounds per acre: about 70 pounds per acre of grayling and 7 pounds per acre of trout. In 1954, the standing crop was approximated at 71 pounds per acre of grayling and 8.3 pounds of trout.

Both the grayling and the hybrid trout spawned in all four tributaries and in the outlet of Grebe Lake between mid-May and late June. Stream temperatures at this time ranged from 40° F. to 57° F. Weirs or blockades installed in the waterways during early May to count spawning migrants provided a means for enumeration of 7,081 grayling and 674 trout in 1953 and 7,878 and 405, respectively, in 1954.

Length-frequency polygons of the grayling spawners showed that females averaged smaller than the males. Lengths of the hybrid trout were variable and no strong modes were evident when lengths were plotted against numbers.

Males of the grayling outnumbered the females in early spawning runs each year. The ratios assumed a more nearly 1-to-1 proportion as the seasons progressed. For this species overall sex ratios in Grebe Lake during 1953 were 10 females to 24 males and, in 1954, 10 females to 9 males.

The natural fry production in Grebe Lake in 1954 was approximated as 236,500 or 2.5 percent of the estimated number of eggs produced by the spawning adults. The greatest mortality during this time was attributed to dislodgment of the eggs during the incubation period either by subsequent spawners or by changes in water level and current velocity.

Scales for age-and-growth analyses were collected from both the grayling and the hybrid trout throughout the study period. The time of annulus formation for grayling younger than 3 years was found to be prior to June 25. No scales from 3-year-olds less than 13 inches in total length had an evident annulus during the spawning season. The interpretations of scales from the grayling more than 3 years of age were considered inaccurate because of the small annual growth in body and scale lengths which in some samples either had obscured the correct interpretation of existing marks or had precluded annulus formation entirely. An additional complication often resulted from a failure of annulus I to form on individuals which had been too small to have had scales at the start of their second growing season.

None of the grayling matured before reaching age-group III. The legal size of 6 inches was attained by all during their second summer of life. Averages of the calculated total lengths in inches for the grayling at the end of their first 3 years of life were: I, 4.4; II, 8.9; III, 11.2.

Females of the trout grew faster than did the males and had matured at the start of their fourth summer of life (age-group III). Some mature males of age-group II appeared in the spawning runs. The legal size limit of 6 inches was reached either in the second or the third year of life. Some trout were also too small to have had scales at the end of their first summer and consequently lacked their first year mark. The average calculated total

lengths in inches at various annuli for the hybrid trout in 1953 and 1954 combined were: I, 3.7; II, 7.2; III, 10.5; IV, 12.8; V, 14.9; VI, 17.3; VII, 17.5.

The length-weight relation for the grayling was determined to be log weight=2.7682 log length −1.2925, and for the hybrid trout log weight= 2.5420 log length−0.9674, where weights are in hundredths of a pound and lengths are in tenths of an inch.

The food of the grayling during its first summer of life consisted of small nymphs of aquatic insects, amphipods, and *Daphnia*. By the middle of their second summer, young of the grayling were feeding on the same organisms as the adults except for some of the large Odonata of a size too great to be ingested. Diptera larvae and pupae were the major food items found in 40 of the grayling and 10 of the trout from Grebe Lake during the 1952 to 1954 seasons.

From a voluntary creel census on Grebe Lake the following estimations of fishing pressure were made. In 1953, 780 fishermen removed 2,148 fish. During 1954, 818 anglers caught 2,863 fish. The catch the first year was 3.1 fish per fisherman, the second, 3.5. Fishing pressure on Grebe Lake was light during the two seasons with a harvest of 7.1 percent of the estimated population or about 6 pounds per acre in 1953, and 9.9 percent or approximately 8 pounds per acre in 1954.

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