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RACES OF CUTTHROAT TROUT IN YELLOWSTONE LAKE

By

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Most trout populations in the United States are not well suited for studies on races because of our lack of knowledge of their identities. Since before the turn of the century, American fishery workers have energetically introduced trouts into barren waters and added to already existing populations. This has resulted in hybridization between species, interbreeding of subspecies, and the mixing of races, both in nature and in fish cultural establishments. Records have been poorly kept or lost in many instances, so the resulting trout populations in most of our waters are not accurately known as to origin, and studies on established races would be most difficult to approach.

In many cases where exact identities are known, the trout have been introduced so recently that there has not been sufficient time for races to separate or form. In other instances where pure stocks were recognized, they have recently become extinct, as with the Utah cutthroat, Salmo clarki utah Suckley, and the Lahontan cutthroat, Salmo clarki henshawi Gill & Jordan (Miller, 1950).

Yellowstone Lake in Wyoming supports a stock of the Yellowstone cutthroat, Salmo clarki lewisi (Girard), that has remained free of the influences of any trout from outside the drainage. No other species of trout have been introduced, and no cutthroat from other waters have entered the lake or its tributaries, save perhaps a small number of Snake River cutthroat that may have wandered in through the original avenue of natural stocking.

The cutthroat in Yellowstone Lake, then, is admirably fitted for studies on its races. The stock has been virtually pure for a long time, the geography is well adapted for such studies, and enough biological investigation has been carried on to provide a moderate accumulation of facts on which to base an inquiry into the formation and existence of races.

TERMINOLOGY

Many terms have been used to designate taxonomic groups of animals below the species level. The subspecies is the most widely used such designation in zoology, and is defined by Mayr, Linsley, and Usinger (1953) as "geographically isolated aggregates of local populations which differ taxonomically from other such subdivisions of a species." Other names are sometimes used synonymously with the term "subspecies", the term "race" being in use by many groups of zoologists. Fish terminology often utilizes the "race" in designating populations within the subspecies, and it is in this sense that the name "race , or "local race" is used here. Other names, such as "sub-population, might be used, but not the term "subspecies", since it is obvious that we are dealing with separate populations within a group considered by ichthyologists to be a valid subspecies.

Races have been described in several ways. The "geographical race" is localized geographically, and the "ecological race" is localized ecologically. However, since no two localities are alike ecologically (Mayr, et al, 1953), the two are alike. "Physiological races" are those which differ from related populations in some physiological way, as with "temperature races" Temperature races are those having particular temperature preferences or tolerances, and are common in fish, whose dependence upon the temperature of the environment is greater than that of warm-blooded animals. Other physiological races differ from their close relatives

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in factors of sex and reproduction, and are known as "sex races". Ecological races of other kinds have been described as "seasonal races" which cannot mate with other races because the times of reproduction do not coincide, and "altitudinal races", which are races separated altitudinally from others.

Salmo clarki lewisi in Yellowstone Lake probably is divided into races of several of the kinds noted above. It may be that races should not be differentiated so delicately, since many are considered to be synonymous. The fact remains, however, that factors of time, space, and ecology are involved here, and must be used in the analysis to elaborate on the existence of local races.

YELLOWSTONE LAKE

Yellowstone River originates atop the Continental Divide, draining to the north from Atlantic Creek and Two-ocean Pass. After flowing about 30 miles northward, the river enters Yellowstone Lake (fig. 1). The Yellowstone River drains from the north end of the lake and flows approximately 15 miles before reaching the Upper Falls of the Yellowstone, an impassable barrier 109 feet in height. Two-ocean Pass is also the origin of a branch of the Snake River, flowing to the west from Pacific Creek.

Yellowstone Lake lies at an altitude of 7,750 feet above sea level, and is 139 square miles in area. The lake is divided into several large arms and bays, and its irregular shoreline measures over 100 miles. Approximately 35 tributary streams enter the lake, and most of them support the spawning of cutthroat trout. The Yellowstone River below the lake is also used by trout for spawning.

The streams tributary to Yellowstone Lake are diverse in size, in temperature patterns, in flow, and in their chemistry. Many of them receive discharges from hot mineral springs, and high temperatures and pollution intolerable to cutthroat are present at some times in many streams. This diversity in the environment of the trout appears to have had some bearing on the formation of races within the lake and stream system. Variations in physical and chemical conditions also exist from place to place in the lake, and the distribution of groups of fish in the arms of the lake may be related to such environmental differences.

The Yellowstone cutthroat apparently came to Yellowstone Lake from the west, despite the fact that the lake lies east of the Continental Divide and drains into the Gulf of Mexico via the Yellowstone, Missouri, and Mississippi Rivers. Two-ocean Pass, mentioned above, lies astride the Continental Divide just south of Yellowstone Park. At times waters from the area flow into the Yellowstone and Snake drainages, and a continuous waterway is formed. Evermann (1893), after visiting the area, said, ". . . . . and there is no doubt whatever that trout can and do pass over this divide at will." He further stated, "Evidently Yellowstone Lake and the Upper Yellowstone River were stocked from the west, and almost certainly via Two-ocean Pass. The probability that the outlet of Yellowstone Lake at one time was toward the Pacific, as claimed by geologists, only strengthens this solution of the problem. But if this explains the origin of the trout of Yellowstone Lake, it leaves another equally interesting problem without any explanation, viz., the presence of the blob (Cottus bairdi punctulatus) in Pacific Creek and its absence from Atlantic Creek and the entire basin of Yellowstone Lake." Other theories have been advanced to explain the introduction of trout into this drainage, but, whatever route was used, the fish apparently have been established for a long time. Observers claim that trout today can pass over Two-ocean Pass, but no one holds that there is any considerable traffic across the top. The trout above the falls in the Yellowstone are, therefore, almost isolated in this drainage and represent the taxonomic entity Salmo clarki lewisi in its native waters.

LIFE HISTORY

The Yellowstone cutthroat in Yellowstone Lake is an adfluvial fish with a life history similar to those of several other inland cutthroats. Eggs are deposited in shallow redds in the gravels of streams tributary to the lake. Upon hatching, the fry may either move immediately downstream to the lake, may linger in the stream for a few months before descending to the lake, may spend the first winter in the stream, or may spend two or more winters in the stream. Most of

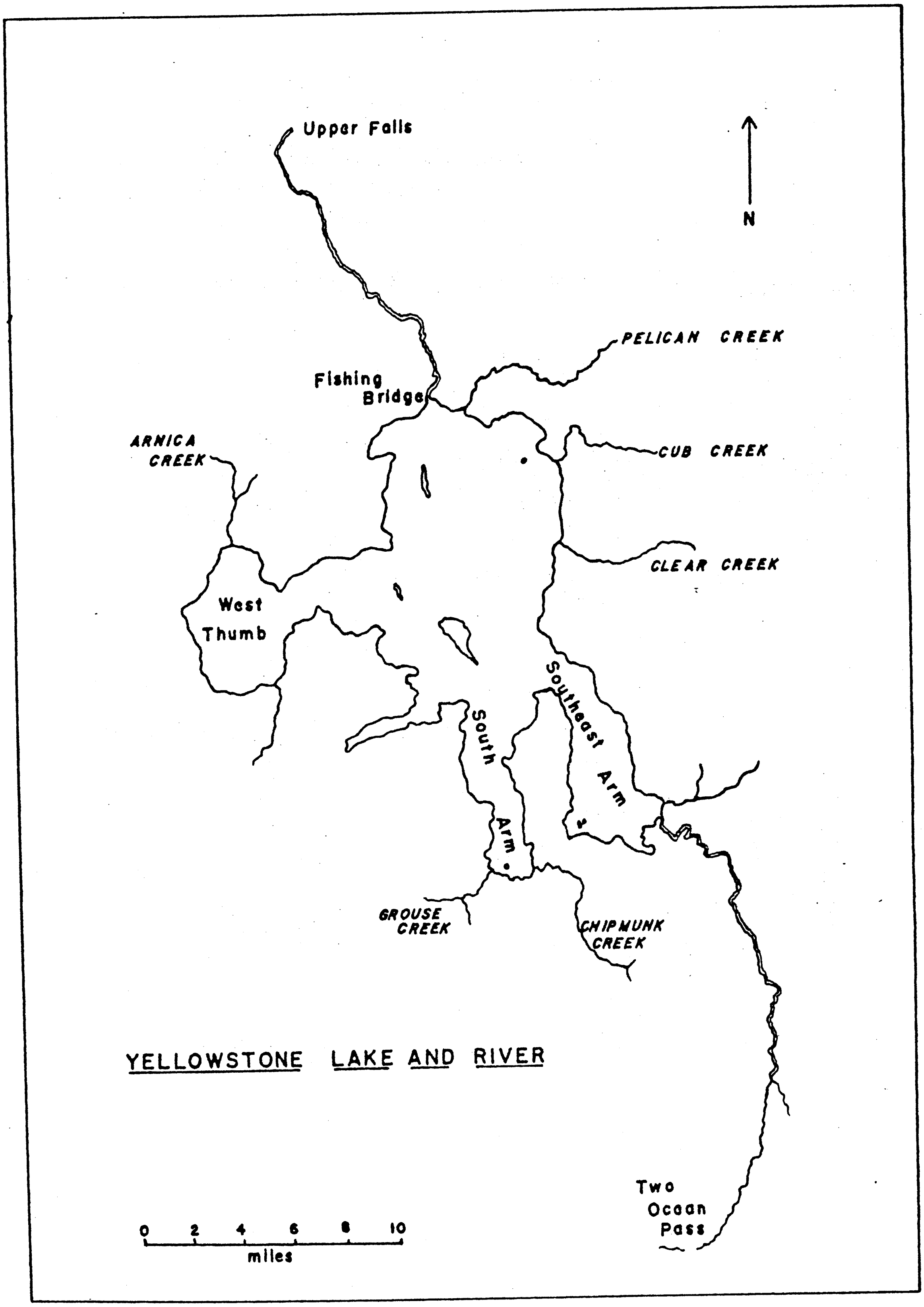

Figure 1.--Map showing the Yellowstone River drainage from Two-ocean Pass to the Upper Falls of the Yellowstone.

the immatures reaching the lake do so in their first season. Development to sexual maturity takes place in the lake, usually in three or four years. At spawning time, the adults ascend the tributary streams, the females dig the nests, spawning takes place, and the survivors of spawning and predation return to the lake. Of those remaining alive the following spring, some will again spawn that season, but a greater number will spawn the year following.

Careful measurements on these tributary streams have shown that mortalities in the egg stage are high, and usually less than one per-cent of the eggs laid will reach the lake as fry. Mortalities are low thereafter, but vigorous predation accounts for many adults, both before and after spawning.

Great distances are sometimes involved in migrations in the lake and in the Lower Yellowstone River, and considerable mixing occurs in the lake with fish from the several spawning streams. Segregation takes place at spawning time, and the spawners return to their natal streams for reproduction.

RACES IN SPAWNING STREAMS

Homing--The study of marked cutthroat at Yellowstone Lake has given an insight into the existence of races that are identified with spawning streams. The demonstration that homing is a strong urge in these populations permits us to recognize races that are distinct from each other geographically, and examination will later show that they are ecologically distinct, as well.

Spawners ascending Pelican, Chipmunk, Grouse, Arnica, and Clear Creeks were marked with Peterson disks in varying numbers. Fish in each of these streams were not marked each year, but from 1949 to 1953, 18,836 tags were applied. The fish were allowed to resume their upstream migrations and spawn, and the survivors were allowed to descend into the lake. After subsequent mortalities in the fishery and from natural causes, some were still alive at the next spawning time. Only 3.2 percent of returning spawners returned to streams other than those in which they were originally tagged. Table 1 summarizes the tag returns to spawning streams.

This overwhelming evidence may not be proof of what is called "homing", since the fish were not marked as immatures before they originally left their natal streams. It does constitute a basis, however, for the claim that each of these populations uses only its own stream, and can therefore be termed a local race. Homing in these fish has been discussed by Ball (1955).

The question may be raised concerning the lake habitat of these fish in support of the view that they may return to their own streams not because of their being part of a particular race, but because they spend their lake existence near the mouths of their own streams and use these streams because they are the closest ones at spawning time. This idea is partly refuted by more tagging evidence. Postspawners from some streams often travel considerable distances in the lake before returning to their streams for a second time. For example, tagged fish from Grouse and Chipmunk Creeks are taken in some numbers in West Thumb, as well as in the South Arm. Many of these are caught off the West Thumb Dock, a distance of 20 miles from the home streams. Fish from all streams are caught in greatest numbers in their own arms of the lake, but many are caught at distances. The distribution of angling pressure is an important point in these cases, affecting the localities of recovery of tagged fish. The evidence is clear that many fish return from great distances, and from other arms of the lake to spawn in their home streams. Tagging has also demonstrated that fish in the Yellowstone River ascend to the gravels near Fishing Bridge and spawn there, and that some fish from the lake move down to these same spawning beds at the same time. Each group then returns to the waters from which it started its spawning migration. Movements of 10 miles are common with these fish.

Another point of importance is that the postspawners from any stream are commonly caught in lake areas harboring fish from other streams. The lake fish are thus a mixture of fish from different streams, and at spawning time the various groups have equal opportunity to seek the closest stream for spawning. What happens, however, is that the groups segregate in the lake, and each race finds its own stream.

fishery at Yellowstone (Cope, 1953). These length data were analyzed without regard for ages of the fish. If we can assume that year-class composition remains fairly constant in the spawning runs from stream to stream, we see that some streams have populations which differ significantly from those of other streams. The 1952 spawning runs into Grouse Creek averaged 374.7 millimeters in mean total length, which is significantly different from the spawners of the Yellowstone River, measuring 367.7 millimeters, those of Pelican Creek, measuring 355.9 and of Arnica Creek, measuring 353.5. Chipmunk Creek characteristically supports the largest spawners of all these streams, and in the years when sampling was good the size superiority was statistically significant.

If racial differences in sizes cannot be claimed for these spawning populations because lengths of fish of like year classes were not compared, then a claim may be made on the basis of differences in age composition of the spawning runs. The fact that the size differences appear from year to year, with the different streams retaining their same relative ranks, suggests that variation in year-class composition may be fairly small from year to year, and that the differences noted above may be related to racial differences in this drainage. Figure 3 illustrates the extent of differences in length for three streams throughout the 1945 season. The same general relationship between these three streams was repeated in 1951, 1952, 1953, and 1954.

The dispersion about the points which control the curves in figure 3 can be visualized from the following coefficients of variation: May 28-29; Chipmunk Creek, 4.09; Grouse Creek, 5.23; Pelican Creek, 7.78. July 2-4; Chipmunk Creek, 5.79; Grouse Creek, 6.47; Pelican Creek, 8.61. July 11-14; Chipmunk Creek, 5.37; Grouse Creek, 5.56; Pelican Creek, 6.90. The sizes of fish at the beginning of the spawning runs are significantly different, from stream to stream, but the significance is lost as the season progresses. The mean lengths of fish in all streams becomes smaller with the progress of the season.

The influence of differential fishing pressures on age and size composition of spawning runs must be considered here. If trout from certain streams are subjected to unusually heavy fishing pressures which take high tolls of the larger and older fish, subsequent spawning runs will probably contain smaller fish. This has been suggested (Cope, 1953) for Yellowstone Lake, where heavy fishing pressures in the north end of the lake appear to have affected the sizes of spawners in Pelican Creek and of fish taken in the Fishing Bridge area fishery. Chipmunk and Grouse Creeks do not seem to have been affected to such an extent. Fish size still appears to relate to racial differences, however, because size differences were measured in the years before fishing pressure became so heavy. Also, compare Chipmunk Creek fish with those of Grouse Creek. The two streams enter the South Arm not far from each other, the postspawners occupy the same parts of the lake and are subject to the same fishing pressure, the populations are usually about the same size, and yet Chipmunk Creek spawners are consistently larger than those of Grouse Creek.

Size differences have also been demonstrated in fish taken from two parts of the lake fishery, the West Thumb and the Fishing Bridge areas. Here we are dealing not with individual races, but with mixtures of races. Fish taken in the Fishing Bridge area fishery (in the northeast part of the lake) are consistently larger than those caught in West Thumb, at the beingning of the season and thereafter. Tagging has shown that fish from certain streams commonly move to certain parts of the lake after spawning, even though the preferred lake habitat may be some distance from the spawning stream. Despite the fact that straying into other portions of the lake occurs to a minor extent, the lake populations in each part of the lake are dominated by fish from the same streams each year. There are, then, certain races of fish associated with particular lake areas, as well as with particular spawning streams, and this holds true from year to year.

Sizes of eggs.--There is not a great deal of morphometric information available from cutthroat in Yellowstone Lake, but there are records pertaining to egg size and numbers that seem to show that fish from different streams bear eggs of different sizes and in different numbers. Keeping in mind the general principle that the

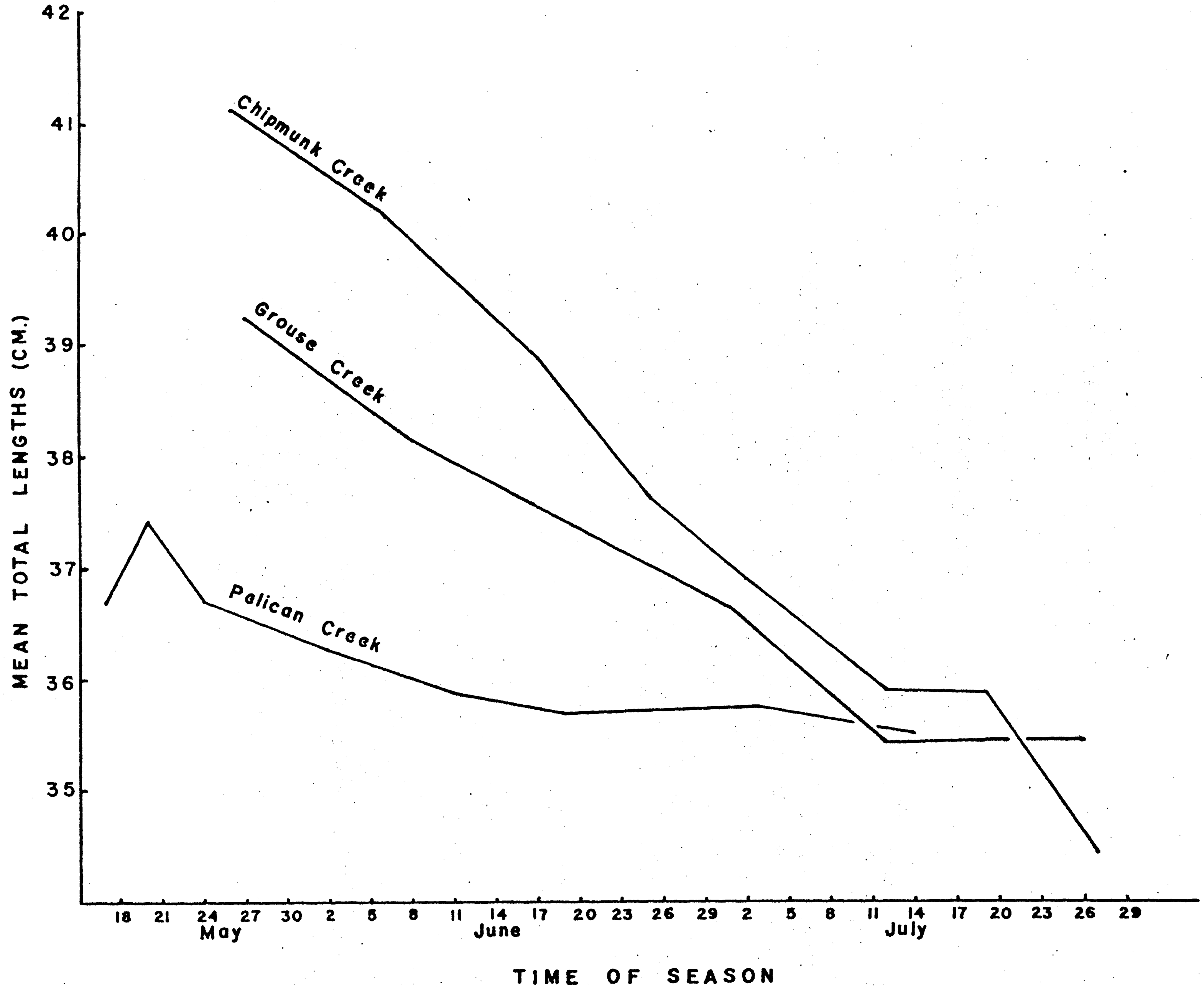

Figure 3.--Distribution throughout the 1945 spawning season of mean total lengths of spawners in three tributaries of Yellowstone Lake.

larger trout produce more eggs and larger eggs than do the smaller trout, we perceive differences in eggs that are independent of the differences in fish size between streams.

Table 2 is based on Yellowstone hatchery egg-taking records for the years 1941 through 1952. We do not have length data for all streams for comparison with the numbers in table 2, but available measurements indicate that Chipmunk Creek fish average among the largest, Pelican and Arnica Creek fish are small, and Grouse Creek fish are intermediate in size. If fish of these streams were all of the same race, we would then expect Chipmunk Creek females to have the largest eggs and the greatest number per female, for Grouse Creek to be intermediate in these relationships, and for Pelican Creek and Arnica Creek females to have small eggs and small numbers per female. The table shows that Chipmunk Creek does, indeed, have the largest eggs (262 per ounce) and Pelican Creek the smallest (307 per ounce), and that Grouse Creek occupies an intermediate position (286 per ounce). Arnica Creek, however, with 268 eggs per ounce, has the second largest eggs on the list, rather than having the small eggs that the fish size would lead us to expect. Chipmunk Creek has a relatively small number of eggs per female (981) instead of the large number we would expect. Pelican and Arnica Creeks, with 979 and 899, respectively, have the low numbers we would expect (but with rather large discrepancy between them), and Grouse Creek has the expected intermediate number (1,007). We are faced with the fact that we do not have length measurements in these streams for all the years from 1941 through 1952, but measurements are available for several of these years, and the relative sizes of fish in these streams have been very consistent through these years.

Figure 4 plots regressions of total numbers of eggs on ovary weight for three streams. These relationships are based on measurements made by Dr. Stillman Wright in Pelican, Chipmunk, and Grouse Creeks in 1945. The trends show that Pelican Creek fish have more eggs per ovary weight than those of Chipmunk Creek, and Chipmunk Creek fish more than those of Grouse Creek. This is evidently not related to size of fish, since Chipmunk Creek fish are larger than are Grouse Creek fish.

Coefficients of regression were calculated for each of the regressions in figure 4, and then compared according to the method described by Simpson and Roe (1939), page 279. These tests, for significance of differences between regression coefficients, resulted in the following t values: Grouse Creek vs. Pelican Creek - 17.207; Grouse Creek vs. Chipmunk Creek - 8.774; Chipmunk Creek vs. Pelican Creek - 8.166. These values indicate that the relationship for each stream is very significantly different from that of each of the other two streams.

These relationships involving eggs appear to show that the fish of certain streams have specific characteristics that are different from those of adjacent streams as well as remote streams.

SUMMARY

Yellowstone Lake and the Upper Yellowstone River, and possibly part of the Upper Snake River drainage, form a closed system. The Yellowstone cutthroat is held within these waters, and no introduction has been made within the history of fishery work. These fish are thus suited to studies on races. Several spawning tributaries to Yellowstone Lake and the river have been studied to determine the existence of distinct races in this drainage.

The association of groups of fish with particular spawning streams has been established through tagging. Homing to streams occurs in 97 percent of the spawners, suggesting that each stream has its own race of trout. Migrational patterns in the lake after spawning are quite constant from year to year, races from certain streams often moving great distances. Mixing of races takes place in the lake, and each part of the lake appears to contain about the same mixture each year.

Times of migration into five streams were examined for a five-year period, and five different patterns were perceived. The patterns were very constant from year to year, some streams supporting early runs, some late runs, some having bimodal distributions, and

Table 2.--Some characteristics of cutthroat eggs taken for the Yellowstone hatchery, 1941 through 1952

Stream	Total eggs taken	Total number of females	Total weight of eggs (ounces)	No. eggs per female	No. of ounces per female	Number of eggs per ounce
Pelican Cr.	53,125,206	54,292	173,135	979	3.189	307
Cub Cr.	9,406,065	9,479	33,805	992	3.566	278
Clear Cr.	39,609,160	38,917	144,788	1,018	3.720	274
Columbine Cr.	18,580,614	18,948	66,890	981	3.530	278
Chipmunk Cr.	54,298,802	55,368	206,853	981	3.736	262
Grouse Cr.	36,990,787	36,726	129,305	1,007	3.521	286
Hatchery Cr.	4,263,388	4,111	14,855	1,037	3.613	287
Arnica Cr.[1/]	4,599,998	5,116	17,185	899	3.359	268

1/ These records cover the years 1936 through 1940

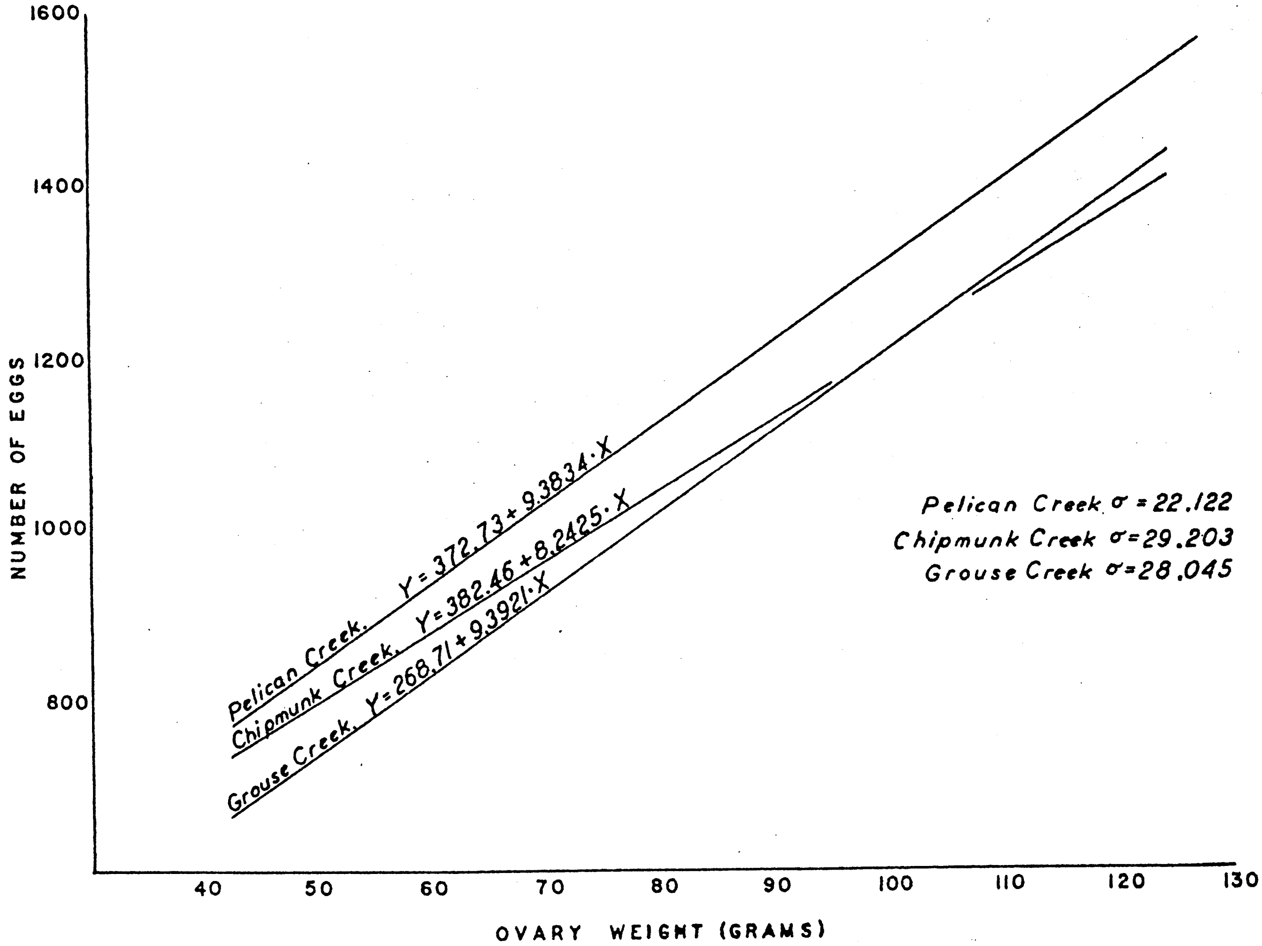

Figure 4.--Regressions of numbers of eggs on ovary weight for females in the 1945 spawning runs of three Yellowstone Lake tributaries.

some having essentially a single mode. Water temperature records were examined in connection with times of migration, and there appears to be a relation between the two. Of the fish in the lake, however, only those of a certain race will segregate and respond to the stream temperatures of its own stream. These races might, then, be geographical races, ecological races, or temperature races.

Differences in mean total length of fish in spawning runs have been measured, and significant differences found between streams The differences may be due to differences either in age composition or in growth rate, but in either case they would be racial differences, since sizes of fish in different streams bear the same relationship to each other year after year. Size differences have also been compared for fish caught in two areas of the lake, and have been found to be significantly different.

Sizes of eggs and numbers of eggs per female from eight streams were compared in relation to sizes of fish. Counts and measurements did not always correspond to the figures that would be expected if the fish were all of the same race. Some streams had small fish with relatively large eggs, suggesting that some races diverged from the general relationships to be expected. Difference in numbers of eggs per unit of ovary weight were measured among three streams.

Acknowledgment is made of the data on egg numbers and ovary weight collected by Dr. Stillman Wright, of the records on hatchery egg take provided by Mr. William Dunn, Superintendent of the Yellowstone hatchery, and of the fish counts and measurements secured by many fish culturists and biologists of the U.S. Fish and Wildlife Service. Mr. Martin Laakso, Fishery Research Biologist at Logan, very kindly aided in checking computations.

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