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THE SPAWNING HABITS OF BROOK, BROWN AND RAINBOW TROUT AND THE PROBLEM
OF EGG PREDATORS

John R. Greeley

INTRODUCTION

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FISH DIVISION

The problem of the success of natural reproduction of trout is one of considerable interest to the fisheries investigator. The question of destruction of trout eggs by various enemies, conspicuously the sucker and other so-called "coarse fishes" has often been discussed before this society. Incontrovertible evidence, from stomach examinations, has shown that the common sucker and the bullhead do devour lake trout eggs (Atkinson 1931, Greene, Hunter and Senning 1932). The presence of common suckers on brook trout spawning beds at night has been recorded (Barbour 1930).*

During the fall and spring of two years, 1930-31 and 1931-32, the writer carried on a field study of the spawning behavior and spawning conditions of trout in some streams of western Michigan (Lake, Osceola and Manistee counties) for the purpose of determining the severity of destruction of trout eggs by natural enemies. This work was done at the request of the Department of Conservation.

The first step in this investigation was to determine how trout, of each of the three stream species of the region, carry on their reproductive activities.

*Mr. Barbour's paper does not make clear what species of trout and sucker were involved but he has written me identifying the fish as Salvelinus fontinalis and Catostomus commersonii.

No accurate evaluation of the detriment to trout that may be caused by egg eaters can be made without knowing, with exactness, how the spawning takes place. To this end, many hours were spent in observing the breeding behavior of the wild trout, under natural conditions. Meanwhile, particular attention was given to the behavior of any possible egg predators.

The reason for pursuing this method of study, rather than the stomach examination method, is that the finding of eggs in a stomach does not prove to be evidence of an act destructive to trout reproduction. This point will be discussed later.

Although it was not possible to carry on the investigation in streams representative of all regions of the state, records were made at eight different spawning places, streams of the Pere Marquette, Sauble, Little Manistee and Manistee drainage basins. Since common suckers, and other possible spawn eaters are present in each of these stream systems it was thought that the sample would include some streams subject to heavy egg predatism, provided this existed.

Brook trout (Salvelinus f. fontinalis) were studied on the following days: November 12 and 13, 1930; October 24, November 3, 4, 5, 7, 8, 24 and 25, 1931; and December 5 and 6, 1931. Brown trout (Salmo fario) were studied: November 12 and 13, 1930; November 4, 5, 8, 24 and 25, 1931; and December 6, 1931. Rainbow trout (Salmo gairdnerii irideus) were studied: April 9-19 (inclusive) 1931; May 2 and 3, 1931 and April 23, 1932. The rainbow trout (steelhead trout) represented the Lake Michigan population, which ascends streams of western Michigan during the spawning run. The brook and brown trout were stream-resident fish.

Mr. Gerald McCrimmon, who was engaged in tagging trout during the fall of 1930 and 1931 for studies of trout migration being carried on by the Institute for Fisheries Research, cooperated in the investigation of predators. Prof. T. L. Hankinson, of Ypsilanti Normal School contributed the photographs used as illustrations.

THE SPAWNING HABITS OF TROUT

The salmons and trouts are nest-building species, which spawn in gravel nests, commonly termed redds. While much has been published about trout reproduction (particularly the work of Kendall 1929 and White 1930 on brook trout, Malloch 1910 on brown trout, and Seagle 1897 on rainbow trout) there yet remain many facts to be learned concerning the breeding behavior of any species of trout or salmon. The observations of the present writer have been in agreement with several published statements regarding the processes of nest building and nest defense but have not agreed with any descriptions of the spawning act, the most critical point in the breeding behavior, from the standpoint of an investigation of egg predators.

The brook and brown trout spawning grounds were all located in spring streams, near sources of spring water. At two streams, Baldwin Creek and Sandborn Creek, both species were using the same spawning places at the same time. The factors governing the spawning places of brown trout are evidently in rather close agreement with those discussed for the brook trout by White (1930). The rainbow trout grounds ranged from headwater spring streams such as Baldwin Creek, previously mentioned to be used in fall by brook and brown trout, to large, lower-course streams such as the Manistee River below Wellston. The river here becomes too warm for trout in summer, the water being remote from its spring-water sources. All spawning grounds were alike in having gravel present.

Each of the three species of trout has a long spawning season at any one locality studied. During 1931 brook trout were breeding at Baldwin Creek (Lake County) during the period from October 24 to December 6, 1931. Brown trout at Sandborn Creek (Lake County) were present on spawning grounds from November 4 to November 25, 1931. Rainbow trout were spawning in the Little Manistee River (Lake County) from April 9 to April 19, 1931. The breeding period of this, and doubtless of the other two species, is longer than that indicated by the dates

given. Seasonal variation is to be expected and, during the mild winter of 1931-1932, rainbow trout began reproduction by January in the Little Manistee River. On April 23, 1932 spawning fish, eggs in several stages of development, and fry which had absorbed the yolk sac were taken in this stream.

Recovery of 11 tagged brook trout (9 males and 2 females) at Little Beaver Brook (Osceola County) showed that an individual of either sex may remain on the spawning grounds for as much as 25 days. A single male rainbow trout which was tagged on a spawning ground in the Little Manistee River was recovered at the same place six days later.

Individual fish vary in the time of arrival at spawning places, probably due to differences in time of maturity. At Little Beaver Creek, during November 1930, after the greater proportion of the brook trout in this small stream had been marked by tagging and no unmarked fish could be taken for a few days, there soon came a heavy run of new individuals, of both sexes.

At any one spawning place, there were more males than females to be seen. The explanation of this fact is attributed, in part, to a younger average maturity of the males and, in part, to a difference in behavior. Females were rarely seen unless actually engaged in nesting activities. Males, on the other hand, frequently remained for long periods in the shallow water of the spawning places or swam boldly about, as though in search of females. The activity of males results, in many cases, in the clearing of sediment from large areas of gravel. The digging of a spawning pit is exclusively a phase of female behavior, however.

Trout spend many hours in construction of a redd and only a few seconds in spawning therein. Even when the most active redds were selected for study, a single observed spawning per day of field work was more than could usually be expected. While scores of brook and rainbow trout redds and dozens of brown trout redds were seen, the spawning of brown trout was observed but once, of brook

trout but twice, and of rainbow trout but seven times.

The hours of greatest activity were found to fall within the daylight period. The single observed spawning of brown trout took place at 1:45 p.m. Brook trout records, of spawning or of early stages in redd covering, fell between 11:30 A.M. and 4:45 P.M. (six records). Both of these species were more active during the mid-day period when the light was brighter than in the early morning and late evening. The rainbow trout was found to be the direct opposite in that their redds were deserted during the mid-day period, on all days of bright sunlight. Rainbow trout spawning observations were as follows: 10:30 A.M. (one record) and 4:30 to 6:45 P.M. (six records).

In view of published statements regarding the presence of egg eaters on trout beds at night (Atkinson 1931, Greene, Hunter and Senning 1932, Barbour 1930) it was thought desirable to determine whether spawning took place at night in these Michigan streams. Several night visits were made to brook and rainbow trout redds ~~which had been used by fish during the preceding daylight trout redds which had~~ been used by fish during the preceding daylight period. Although brook trout were seen under shelter of logs near the spawning areas, none was observed on redds during a visit to the Baldwin Creek beds from 9 to 11 P.M. on November 3, 1931. Attempts to find rainbow trout working redds where they were seen by day failed to produce evidence of fish, at the Little Manistee River on two evenings in April 1931. Marked redds of all three species failed to show evidence of night activity since no change occurred at these during the period between late afternoon and the following morning. Evidently digging of redds had not been continued during the night. Rainbow trout females which have spawned during the period just before dusk evidently remain on redds part, if not all, of the hours of darkness.

For purposes of the study of the relations of egg predators to trout, the very complex behavior of trout, of the three species, may be summarized:

A. Behavior preceding spawning. The female selects a place where there is

gravel and digs a deep pit, by repeated use of the tail. In digging, the fish turns on one side and strikes the tail rapidly downward against, or close to, the gravel. Sometimes as much as two days are spent in digging a redd. Interruptions occur, with frequent desertions. The finished pit varies in size according to species and size of female, current conditions and type of bottom. Brown and rainbow trout spawning pits are, on the average, larger than those of brook trout, the difference being partly due to size of females. In all instances the hollow which was constructed was longer than the female making it and deeper than the greatest body depth of this fish.

Nearby males are quickly attracted to females engaged in digging. One male, of brook or brown trout, attends a female, and stations himself just downstream of her. He defends this position against other males except when an invading male of larger size than he succeeds in driving him away. Rainbow trout redds, in stages near the time of spawning, have two males the larger of which permits a smaller one to occupy a position just downstream.

A long period of courtship is characteristic of the behavior before spawning takes place. A male attending a female frequently advances forward to a position close to or touching her side. Frequently this is done during an act of digging by the female and one might easily interpret the fish to be spawning. The prolonged period of digging and courtship behavior is evidently responsible for the interpretation of the spawning act as described by several observers of brook and brown trout (Kendall 1929, Malloch 1910).

Both male and female trout defend the redd against other fish in the period just preceding spawning. Defense by the male, against rival males which approach from downstream or from the side is very vigorous. Any invading fish are chased by either male or female, depending upon which part of the nest they approach. The female quickly notices and chases fish which approach from upstream, but does not seem to take notice of ones downstream of her.

B. The spawning act. A single act of spawning occurs at a single nest pit. There is a definite mating clasp that is different from any of the phases of behavior which preceded spawning. The change in behavior of the female immediately after the eggs have been deposited is conspicuous.

Before spawning, the female takes a position at the bottom of the pit, with pectoral and ventral fins well spread against the stones. She remains motionless with her vent region close to the deepest part of the pit. Of brook and brown trout, the male, a larger fish than the female at all observed instances of spawning, darts to a position against one side of the female and curves his body toward hers in such a manner as to hold her against the bottom. For several seconds there is a rapid vibration of the body of the male. The spawning position of a female rainbow trout is similar to that described for those of the other species except that, upon coming into position, a female rainbow trout opens the mouth. (Experiments with a freshly-killed female proved that the open mouth was of aid in permitting the fish to stay in the spawning position, since the open mouth increased the current resistance of the normally stream-lined body of the fish. The fins, being spread, prevent downstream slipping so that the current-thrust which acts against the open mouth wedges the fish into a firm position. This was duplicated with the dead specimen, which remained in position indefinitely, provided the mouth was wedged open). The two rainbow trout males, one slightly larger than the female and ^{the} other, typically, a younger, smaller male not so large as either fish, quickly take positions, one at either side of the female. As they come into place, with fins spread against the bottom, they open their mouths. Both are seen to be tightly wedged against the female, the tails of the grouped fish being in close contact. The force of the current, acting against the open mouth of each male, is transmitted into a strong pressure against the sides of the female as the three fish remain motionless for approximately five to ^{eight} ~~either~~ seconds. An appreciable cloudiness of the water

doubtless caused by milt from the males, was noted at one nest. Although eggs could not be seen when deposited at any of the trout redds, their presence was verified by excavation of the exact spot where spawning was noted.

The number of eggs deposited at a single spawning at two brook trout redds dug out immediately after the spawning was 40 and 79 respectively. A single brown trout redd gave a count of 38 eggs. A single count at a rainbow trout redd, the highest of several other counts not given because of uncertain accuracy, was 855 eggs. Only by digging with a sharp-edged implement, such as a shovel, and by lifting the eggs and gravel well, before shaking into a net held below, could the entire number of eggs be secured. Attempts to dig out eggs with the hands were unsuccessful for the gravel was disturbed in a manner such as to allow eggs to sink deeply into crevices between the rounded stones.

All of the eggs fall amid large gravel or even large stones as much as four inches in diameter, at a limited area of the nest bottom, which is from two to over twelve inches below the level of the normal stream bottom. Evidently only a few escape from the pit and are carried downstream (the evidence for this conclusion will be discussed later).

C. Behavior following spawning. Immediately after spawning, a female commences to cover the eggs with gravel. Brook trout females begin to do this by a slow and rhythmic swinging of the body from side to side, as if swimming slowly, but with a greater sweep of body than used in normal swimming. The tail and anal fin are pressed against the gravel and effectively move loose pebbles inward toward the center of the pit. The eggs are soon entirely covered with coarse gravel. After a half hour or more of this behavior, females were noted to begin digging at an area a few inches upstream of the eggs. The fine gravel thus stirred up is deposited over the redd by the current. Brown and rainbow trout females begin to cover eggs by rapidly digging with the tail,

moving the loose, coarse gravel of the bottom just upstream of the eggs. After a large amount of gravel has been piled on the eggs, the fish use the tail and anal fins in a sweeping process which is much like, but less pronounced than, that used by brook trout females in beginning to cover eggs.

Male defense lasts only through early stages of egg covering. By the time males desert, which they do within about five minutes of the time of spawning, an effective but unfinished coating of gravel has been placed over the eggs. The absence of the male exposes the area downstream of the nest to invasion by other fish. The female, however, throughout the long period of egg covering (a process continued for one to several hours) resents the presence of any fish at or just above the spot where the eggs lie.

A female remains for several hours or more at the former spawning pit which is finally so covered as to be indistinguishable, the eggs being overlain by one and a half to over eight inches of gravel. Coarse gravel immediately surrounds the eggs while finer gravel usually forms an outer coat, especially in brook trout redds.

Both males and females participate in several mating acts before becoming entirely finished with the reproductive activities of a single season. Partially spent females and males were dissected. The dissection of several males showed that the anterior lobe of the testis was later in maturing than the posterior lobe. Several partially spent female brook and rainbow trout, identifiable as individuals, dug redds just upstream of their first ones.

WASTE EGGS AND NON-WASTE EGGS

Any eaters of trout spawn must get the eggs by one or more of the following means: (1) By rushing in and securing eggs at the moment of deposition; (2) By digging out eggs after they have been covered. (3) By taking stray eggs which are not within a redd pit.

There are normally a few eggs at a spawning which fail to lodge in the cup of the redd and escape, being carried downstream by the current. Although such eggs could not be seen, the behavior of fish, attracted by this source of food, showed the presence of stray eggs. At three brook trout redds, small brook trout picked up one to several objects just downstream of the point where spawning had occurred a few minutes before. The small percentage of eggs which escape from the redd during spawning or early stages of egg covering may be termed waste eggs. Unprotected from light and mechanical injury, they are obviously of no value to the species. The eating of such eggs is to be regarded as harmless scavenging.

Trout of all three species were seen to dig redds on or near the exact spots previously used by other individuals. While virtually impossible to observe, because of the difficulty of seeing the eggs, there is a strong probability that some eggs are dug out of the older redds by the builders of new ones. The percentage dislodged by this accidental means is not large on the spawning grounds studied. This occurrence, however, doubtless adds to the number of waste eggs available to egg eaters. Pacific salmon are known to dislodge large numbers of eggs from the gravels (Gilbert and Rich 1927, p. 20, 28).

Stomach examination as a means for investigation of egg predators has a weak point in that, by this method alone, one cannot interpret the circumstances under which the eggs have been taken. If a supposed predator is eating only waste eggs, he cannot be considered to be doing harm to the trout. If, however, the eggs are non-waste, viable eggs, a possibility of damage has been proven. The study of whether or not serious damage exists is then in order. This will involve quantitative studies for it is the number remaining that is important, not the number eaten. Even in the event that a large percentage of the total number of viable eggs were to be destroyed, it is possible that enough might remain to produce a number of young sufficient for the carrying capacity of the waters concerned.

EVIDENCES OF EGG EATING

Observations indicated that several species of fishes seemed to get a few trout eggs. Stomach examinations of certain specimens taken near trout redds supported this evidence.

Muddlers (Cottus cognatus and Cottus bairdii). These small fishes, particularly Cottus cognatus were present in nearly all of the streams studied. Single individuals were seen near several brook and rainbow trout redds. They evidently make attempts to get trout eggs, for they were sometimes seen to dart in toward the place where a female brook or rainbow trout was engaged in the process of covering eggs. At two brook trout redds and one rainbow trout redd, the invader was immediately discovered and pursued by the female. In no instances was eating of eggs observed. A single specimen of C. cognatus, however, which was secured from a brook trout redd proved to have a single trout egg in its stomach. This was probably a stray egg or else an egg stolen before covering had been completed. Although muddlers will dig under stones, it hardly seems likely that they can dig deeply enough to secure trout eggs after these are completely covered.

Common sucker (Catostomus commersonii). Surprisingly few suckers were seen about the spawning grounds of the trout. A single one, not over eight inches long, was seen at a rainbow trout redd on the Little Manistee River. Several were noted in deep pools on this river and on Baldwin Creek near the riffles used by spawning rainbow trout. Probably the one sucker observed at the rainbow trout redd, mentioned previously, succeeded in finding one trout egg for he swam slowly about just below the place where spawning had been observed a few minutes before, stopped and apparently ate something from the bottom, and then swam out of view. Obviously, if this fish did find an egg it was a stray one.

Brook trout (Salvelinus fontinalis). Small, mature males of brook trout were numerous on the Baldwin Creek and Little Beaver Creek grounds. Such individuals were the most abundant of the egg eaters. At three different redds

the visits of one or more brook trout took place just after spawning had occurred. Searching the gravel just below a redd, and picking up one to several objects invisible to the observer, these fish apparently secured a few stray eggs. Several attempts to rush to the position occupied by the female covering eggs were immediately resented by this fish. A few brook trout eggs found in stomachs of three trout, taken at random from Little Beaver Creek, supported the interpretation of this species as an egg eater. Large numbers of brook trout eggs in trout stomachs have been recorded (White 1930).

Brown trout (*Salmo fario*). It is probable that the smaller brown trout may be successful in picking up a few of the eggs of their own species, under circumstances similar to those described for brook trout. Several brown trout, seven to nine inches in length, taken from the Little Manistee River during April 1931, contained rainbow trout eggs. Small brown trout were noted, upon several occasions, just below rainbow trout redds.

Rainbow trout (*Salmo gairdnerii irideus*). The most numerous of the possible egg eaters seen around rainbow trout redds on the Little Manistee River were juvenile rainbow trout of six to eight inches. One of these was seen to rush in during the spawning clasp of a trio of rainbow trout and he had opportunity, and doubtless made use of this, to take one mouthful of eggs before being chased by the male nearest him. Since 855 eggs were discovered in the pit of this redd, the greatest possible number that could have been stolen by this fish was a very small percentage of the number which were successfully buried by the female. The chasing of small rainbows which attempted to reach the position occupied by a female which had recently spawned was frequently seen. Search of the area below the nest was not prevented by female rainbow trout and the eating of a few objects presumed to be eggs took place here at the majority of the redds where spawning was seen. Metzelaar (1929) found rainbow trout eggs to be frequently eaten by the same species.

Miscellaneous. Although horned dace were present in several of the streams, they were not seen near trout redds. Black-nosed dace, and several other small species which were present in certain of the streams, have too small a mouth to allow them to feed upon trout eggs. No egg predators other than fishes were seen. While one might suppose that the large numbers of breeding trout that were present (as many as 75 brook trout were seen from one observation point at one time) would attract various fish eaters, evidence of any concentration of these was lacking. The spawning season of trout does not coincide with the season of greatest abundance of fish-eating birds, although the American merganser, Osprey, Kingfisher, and Great Blue Heron were among the birds seen during the April studies. Mergansers and other birds are known to feed upon eggs of Pacific salmon when large numbers are available (Munro 1923).

SUMMARY

(1) The relation of the common sucker and other possible predators of trout eggs to trout reproduction was studied by field observations in some western Michigan streams used as spawning grounds. The breeding behavior of brook, brown and rainbow trout was studied.

(2) Female trout construct a pit and deposit eggs at the bottom of this, among coarse gravel or even large stones, during a single act of spawning. One male brook or brown trout mates with one female. Rainbow trout spawn in trios, one male being firmly pressed against each side of the female while the eggs are being deposited. The nesting process is repeated several times before all of the eggs contained by one female have been deposited.

(3) Immediately after spawning, female trout cover the eggs with a thick coating of gravel. Defense by the male is continued during the early stages of nest covering while the female defends the redd for several hours after spawning.

(4) Attempts of trout and muddlers to take eggs from the pit were successfully prevented by female trout, in the majority of observed instances. At most,

a very slight percentage of the eggs deposited in the pit are taken in the interval between spawning and covering of the eggs. No attempts to dig out and feed upon eggs in the finished, covered redds were seen. By the time the female trout desert the eggs these are so well covered by gravel that disturbance by predators is unlikely.

(5) Waste eggs are common, due to the fact that some eggs fail to lodge in the pit and because female trout often dig redds at areas previously used by other trout. The percentage of eggs which are loose in the stream rather than firmly lodged in covered redds is not large. The numbers are sufficient, however, to be sought by egg eating fishes, notably the muddler, common sucker, brook trout, brown trout, and rainbow trout.

(6) Since eggs which are loose in the stream are unprotected from light and mechanical injury they are to be regarded as waste eggs, the destruction of which cannot be harmful to trout reproduction. Trout eggs in stomachs are not sufficient evidence for proof of acts harmful to reproduction.

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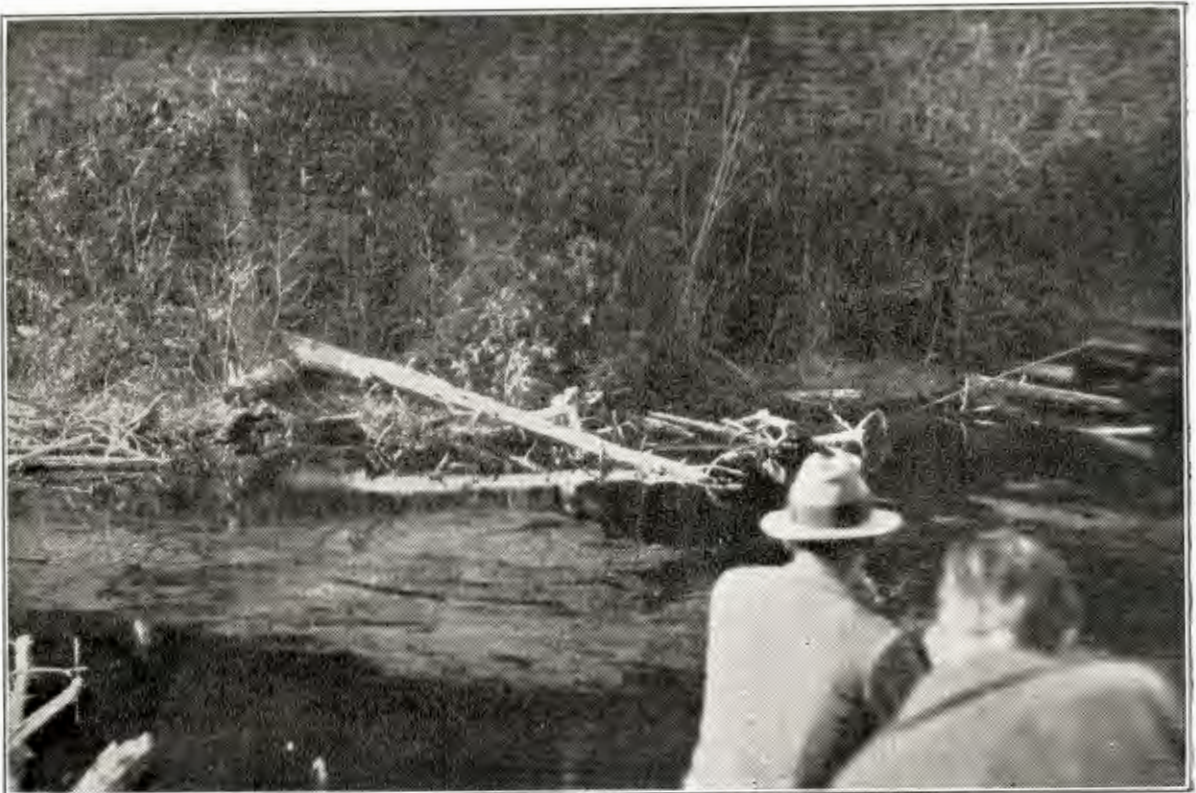


Fig. 1. General view of brook trout spawning grounds, Baldwin Creek. There were six identifiable redds within the large cleared area at the center. Smaller areas of gravel cleaned of muck deposits by the trout may be seen at right of the photograph.



Fig. 2. A brook trout spawning pit which has been completely excavated, ready to receive the eggs, Little Beaver Creek. The deepest part of the excavation is indicated by arrow.

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Individual fish vary in the time of arrival at spawning places, probably due to differences in time of maturity. At Little Beaver creek, during November, 1930, after the greater proportion of the brook trout in this small stream had been marked by tagging and no unmarked fish could be taken for a few days, there soon came a heavy run of new individuals, of both sexes.

At any one spawning place there were more males than females to be seen. The explanation of this fact is attributed, in part, to a younger average maturity of the males and in part to a difference in behavior. Females were rarely seen unless actually engaged in nesting activities. Males, on the other hand, frequently remained for long periods in the shallow water of the spawning places or swam boldly about, as though in search of females. The activity of males results, in many cases, in the clearing of sediment from large areas of gravel. The digging of a spawning pit is exclusively a phase of female behavior, however.

Trout spend many hours in construction of a redd and only a few seconds in spawning therein. Even when the most active redds were selected for study, a single observed spawning per day of field work was more than could usually be expected. While scores of brook and rainbow trout redds and dozens of brown trout redds were seen, the spawning of brown trout was observed but once, of brook trout but twice, and of rainbow trout but seven times.

The hours of greatest activity were found to fall within the daylight period. The single observed spawning of brown trout took place at 1.45 P. M. Brook trout records, of spawning or of early stages in redd covering, fell between 11.30 A. M. and 4.45 P. M. (six records). Both of these species were more active during the mid-day period when the light was bright than in the early morning and late evening. The rainbow trout was found to be the direct opposite in that their redds were deserted during the mid-day period, on all days of bright sunlight. Rainbow trout spawning observations were as follows: 10.30 A. M. (one record) and 4.30 to 6.45 P. M. (six records).

In view of published statements regarding the presence of egg eaters on trout beds at night (Atkinson, 1931; Greene, Hunter and Senning, 1932; Barbour, 1930), it was thought desirable to determine whether spawning took place at night in these Michigan streams. Several night visits were made to brook and rainbow trout redds which had been used by fish during the preceding daylight period. Although brook trout were seen under shelter of logs near the spawning areas, none was observed on redds during a visit to the Baldwin creek beds from 9 to 11 P. M. on November 3, 1931. Attempts to find rainbow trout working redds where they were seen by day failed to produce evidence of fish, at the Little Manistee river on two evenings in April, 1931. Marked redds of all three species failed to show evidence of night activity since no change occurred at these during the period between late afternoon and the following morning. Evidently digging of redds had not been continued during the night. Rainbow trout females which have spawned during the period just before dusk evidently remain on redds part, if not all, of the hours of darkness.

For purposes of the study of the relations of egg predators to trout, the very complex behavior of trout, of the three species, may be summarized:

A. Behavior preceding spawning: The female selects a place where there is gravel and digs a deep pit by repeated use of the tail. In digging the fish turns on one side and strikes the tail rapidly downward against, or close to the gravel. Sometimes as much as two days are spent in digging a redd. Interruptions occur, with frequent desertions. The finished pit varies in size according to species and size of female, current conditions, and type of bottom. Brown and rainbow trout spawning pits are, on the average, larger than those of brook trout, the difference being partly due to size of females. In all instances the hollow which was constructed was longer than the female making it and deeper than the greatest body depth of this fish.

Nearby males are quickly attracted to females engaged in digging. One male, of brook or brown trout, attends a female, and stations himself just downstream of her. He defends this position against other males except when an invading male of larger size than he succeeds in driving him away. Rainbow trout redds, in stages near the time of spawning, have two males, the larger of which permits a smaller one to occupy a position just downstream.

A long period of courtship is characteristic of the behavior before spawning takes place. A male attending a female frequently advances forward to a position close to or touching her side. Frequently this is done during an act of digging by the female and one might easily interpret the fish to be spawning. The prolonged period of digging and courtship behavior is evidently responsible for the

interpretation of the spawning act as described by several observers of brook and brown trout (Kendall, 1929; Malloch, 1910).

Both male and female trout defend the redd against other fish in the period just preceding spawning. Defense by the male, against rival males which approach from downstream or from the side, is very vigorous. Any invading fish are chased by either male or female, depending upon which part of the nest they approach. The female quickly notices and chases fish which approach from upstream, but does not seem to take notice of ones downstream of her.

B. The spawning act: A single act of spawning occurs at a single nest pit. There is a definite mating clasp that is different from any of the phases of behavior which precede spawning. The change in behavior of the female immediately after the eggs have been deposited is conspicuous.

Before spawning, the female takes a position at the bottom of the pit, with pectoral and ventral fins well spread against the stones. She remains motionless with her vent region close to the deepest part of the pit. Of brook and brown trout, the male, a larger fish than the female at all observed instances of spawning, darts to a position against one side of the female and curves his body toward hers in such a manner as to hold her against the bottom. For several seconds there is a rapid vibration of the body of the male. The spawning position of a female rainbow trout is similar to that described for those of the other species except that, upon coming into position, a female rainbow trout opens the mouth.*

The two rainbow trout males, one slightly larger than the female, and the other typically a younger, smaller male not so large as either fish, quickly take positions, one at either side of the female. As they come into place, with fins spread against the bottom, they open their mouths. Both are seen to be tightly wedged against the female, the tails of the grouped fish being in close contact. The force of the current, acting against the open mouth of each male, is transmitted into a strong pressure against the sides of the female as the three fish remain motionless for approximately five to eight seconds. An appreciable cloudiness of the water, doubtless caused by milt from the males, was noted at one nest. Although eggs could not be seen when deposited at any of the trout redds, their presence was verified by excavation of the exact spot where spawning was noted.

The number of eggs deposited at a single spawning at two brook trout redds dug out immediately after the spawning was forty and seventy-nine, respectively. A single brown trout redd gave a count

*Experiments with a freshly-killed female proved that the open mouth was of aid in permitting the fish to stay in the spawning position, since the open mouth increased the current resistance of the normally streamlined body of the fish. The fins being spread, prevent downstream slipping so that the current-thrust which acts against the open mouth wedges the fish into a firm position. This was duplicated with the dead specimen, which remained in position indefinitely, provided the mouth was wedged open.

of thirty-eight eggs. A single count at a rainbow trout redd, the highest of several other counts not given because of uncertain accuracy, was 855 eggs. Only by digging with a sharp-edged implement, such as a shovel, and by lifting the eggs and gravel well, before shaking into a net held below, could the entire number of eggs be secured. Attempts to dig out eggs with the hands were unsuccessful, for the gravel was disturbed in a manner such as to allow eggs to sink deeply into crevices between the rounded stones.

All of the eggs fall amid large gravel or even large stones as much as four inches in diameter, at a limited area of the nest bottom, which is from two to over twelve inches below the level of the normal stream bottom. Evidently only a few escape from the pit and are carried downstream.

C. Behavior following spawning: Immediately after spawning, a female commences to cover the eggs with gravel. Brook trout females begin to do this by a slow and rhythmic swinging of the body from side to side, as if swimming slowly, but with a greater sweep of body than used in normal swimming. The tail and anal fin are pressed against the gravel and effectively move loose pebbles inward toward the center of the pit. The eggs are soon entirely covered with coarse gravel. After a half hour or more of this behavior, females were noted to begin digging at an area a few inches upstream of the eggs. The fine gravel thus stirred up is deposited over the redd by the current. Brown and rainbow trout females begin to cover eggs by rapidly digging with the tail, moving the loose, coarse gravel of the bottom just upstream of the eggs. After a large amount of gravel has been piled on the eggs, the fish use the tail and anal fins in a sweeping process which is much like but less pronounced than that used by brook trout females in beginning to cover eggs.

Male defense lasts only through early stages of egg covering. By the time males desert, which they do within about five minutes of the time of spawning, an effective but unfinished coating of gravel has been placed over the eggs. The absence of the male exposes the area downstream of the nest to invasion by other fish. The female, however, throughout the long period of egg covering (a process continued for one to several hours) resents the presence of any fish at or just above the spot where the eggs lie.

A female remains for several hours or more at the former spawning pit, which is finally so covered as to be indistinguishable, the eggs being overlain by one and a half to over eight inches of gravel. Coarse gravel immediately surrounds the eggs while finer gravel usually forms an outer coat, especially in brook trout redds.

Both males and females participate in several mating acts before becoming entirely finished with the reproductive activities of a single season. Partially spent females and males were dissected. The dissection of several males showed that the anterior lobe of the

testis was later in maturing than the posterior lobe. Several partially spent female brook and rainbow trout, identifiable as individuals, dug redds just upstream of their first ones.

WASTE EGGS AND NON-WASTE EGGS

Any eaters of trout spawn must get the eggs by one or more of the following means: (1) by rushing in and securing eggs at the moment of deposition; (2) by digging out eggs after they have been covered; (3) by taking stray eggs which are not within a redd pit.

There are normally a few eggs at a spawning which fail to lodge in the cup of the redd and escape, being carried downstream by the current. Although such eggs could not be seen, the behavior of fish, attracted by this source of food, showed the presence of stray eggs. At three brook trout redds, small brook trout picked up one to several objects just downstream of the point where spawning had occurred a few minutes before. The small percentage of eggs which escape from the redd during spawning or early stages of egg covering may be termed waste eggs. Unprotected from light and mechanical injury, they are obviously of no value to the species. The eating of such eggs is to be regarded as harmless scavenging.

Trout of all three species were seen to dig redds on or near the exact spot previously used by other individuals. While virtually impossible to observe, because of the difficulty of seeing the eggs, there is a strong probability that some eggs are dug out of the older redds by the builders of new ones. The percentage dislodged by this accidental means is not large on the spawning grounds studied. This occurrence, however, doubtless adds to the number of waste eggs available to egg eaters. Pacific salmon are known to dislodge large numbers of eggs from the gravels (Gilbert and Rich, 1927, p. 20, 28).

Stomach examination as a means for investigation of egg predators has a weak point in that, by this method alone, one cannot interpret the circumstances under which the eggs have been taken. If a supposed predator is eating only waste eggs, he cannot be considered to be doing harm to the trout. If, however, the eggs are non-waste, viable eggs, a possibility of damage has been proven. The study of whether or not serious damage exists is then in order. This will involve quantitative studies, for it is the number remaining that is important, not the number eaten. Even in the event that a large percentage of the total number of viable eggs were to be destroyed, it is possible that enough might remain to produce a number of young sufficient for the carrying capacity of the waters concerned.

EVIDENCES OF EGG EATING

Observations indicated that several species of fishes seemed to get a few trout eggs. Stomach examinations of certain specimens taken near trout redds supported this evidence.

Muddlers (Cottus cognatus and Cottus bairdii): These small fishes, particularly *Cottus cognatus*, were present in nearly all of the streams studied. Single individuals were seen near several brook and rainbow trout redds. They evidently make attempts to get trout eggs, for they were sometimes seen to dart in toward the place where a female brook or rainbow trout was engaged in the process of covering eggs. At two brook trout redds and one rainbow trout redd, the invader was immediately discovered and pursued by the female. In no instance was eating of eggs observed. A single specimen of *C. cognatus*, however, which was secured from a brook trout redd proved to have a single trout egg in its stomach. This was probably a stray egg or else an egg stolen before covering had been completed. Although muddlers will dig under stones, it hardly seems likely that they can dig deeply enough to secure trout eggs after these are completely covered.

Common sucker (Catostomus commersonnii): Surprisingly few suckers were seen about the spawning grounds of the trout. A single one, not over eight inches long, was seen at a rainbow trout redd on the Little Manistee river. Several were noted in deep pools on this river and on Baldwin creek near the riffles used by spawning rainbow trout. Probably the one sucker observed at the rainbow trout redd, mentioned previously, succeeded in finding one trout egg, for he swam slowly about just below the place where spawning had been observed a few minutes before, stopped and apparently ate something from the bottom, and then swam out of view. Obviously, if this fish did find an egg it was a stray one.

Brook trout (Salvelinus fontinalis): Small, mature males of brook trout were numerous on the Baldwin creek and Little Beaver creek grounds. Such individuals were the most abundant of the egg eaters. At three different redds the visits of one or more brook trout took place just after spawning had occurred. Searching the gravel just below a redd, and picking up one to several objects invisible to the observer, these fish apparently secured a few stray eggs. Several attempts to rush to the position occupied by the female covering eggs were immediately resented by this fish. A few brook trout eggs found in stomachs of three trout, taken at random from Little Beaver creek, supported the interpretation of this species as an egg eater. Large numbers of brook trout eggs in trout stomachs have been recorded (White, 1930).

Brown trout (Salmo fario): It is probable that the smaller brown trout may be successful in picking up a few of the eggs of their own species, under circumstances similar to those described for brook

trout. Several brown trout, seven to nine inches in length, taken from the Little Manistee river during April, 1931, contained rainbow trout eggs. Small trout were noted, upon several occasions, just below rainbow trout redds.

Rainbow trout (Salmo gairdnerii irideus): The most numerous of the possible egg eaters seen around rainbow trout redds on the Little Manistee river were juvenile rainbow trout of six to eight inches. One of these was seen to rush in during the spawning clasp of a trio of rainbow trout and he had opportunity, and doubtless made use of this, to take one mouthful of eggs before being chased by the male nearest him. Since 855 eggs were discovered in the pit of this redd, the greatest possible number that could have been stolen by this fish was a very small percentage of the number which were successfully buried by the female. The chasing of small rainbows which attempted to reach the position occupied by a female which had recently spawned was frequently seen. Search of the area below the nest was not prevented by female rainbow trout and the eating of a few objects presumed to be eggs took place here at the majority of the redds where spawning was seen. Metzelaar (1929) found rainbow trout eggs to be frequently eaten by the same species.

Miscellaneous: Although horned dace were present in several of the streams, they were not seen near trout redds. Black-nosed dace, and several other small species which were present in certain of the streams, have too small a mouth to allow them to feed upon trout eggs. No egg predators other than fishes were seen. While one might suppose that the large numbers of breeding trout that were present (as many as seventy-five brook trout were seen from one observation point at one time) would attract various fish eaters, evidence of any concentration of these was lacking. The spawning season of trout does not coincide with the season of greatest abundance of fish-eating birds, although the American merganser, osprey, kingfisher, and great blue heron were among the birds seen during the April studies. Mergansers and other birds are known to feed upon eggs of Pacific salmon when large numbers are available (Munro, 1923).

SUMMARY

(1) The relation of the common sucker and other possible predators of trout eggs to trout reproduction was studied by field observations in some western Michigan streams used as spawning grounds. The breeding behavior of brook, brown, and rainbow trout was studied.

(2) Female trout construct a pit and deposit eggs at the bottom of this, among coarse gravel or even large stones, during a single act of spawning. One male brook or brown trout mates with one female. Rainbow trout spawn in trios, one male being firmly pressed against each side of the female while the eggs are being deposited. The nesting

process is repeated several times before all of the eggs contained by one female have been deposited.

(3) Immediately after spawning, female trout cover the eggs with a thick coating of gravel. Defense by the male is continued during the early stages of nest covering while the female defends the redd for several hours after spawning.

(4) Attempts of trout and muddlers to take eggs from the pit were successfully prevented by female trout in the majority of observed instances. At most, a very slight percentage of the eggs deposited in the pit are taken in the interval between spawning and covering of the eggs. No attempts to dig out and feed upon eggs in the finished, covered redds were seen. By the time the female trout desert the eggs these are so well covered by gravel that disturbance by predators is unlikely.

(5) Waste eggs are common, due to the fact that some eggs fail to lodge in the pit and because female trout often dig redds at areas previously used by other trout. The percentage of eggs which are loose in the stream rather than firmly lodged in covered redds is not large. The numbers are sufficient, however, to be sought by egg-eating fishes, notably the muddler, common sucker, brook trout, brown trout, and rainbow trout.

(6) Since eggs which are loose in the stream are unprotected from light and mechanical injury they are to be regarded as waste eggs, the destruction of which cannot be harmful to trout reproduction. Trout eggs in stomachs are not sufficient evidence for proof of acts harmful to reproduction.

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