MICHIGAN DEPARTMENT OF CONSERVATION
Research and Development Report No. 140 [1]

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SOME FACTORS AFFECTING SURVIVAL OF YOUNG-OF-THE-YEAR BROOK TROUT, *SALVELINUS FONTINALIS* (MITCHILL), IN STREAMS

By W. C. Latta

Abstract

Survival of brook trout during the first year of life was considered in relation to (1) territorial behavior, (2) other segments of the trout population, (3) starvation and (4) the amount of groundwater entering the stream. No relationship was found between abundance of fingerling progeny and the number of spawners. Survival of eggs in the redds is usually high. Although little is known about losses of fry during emergence from the redds, it is presumed that most of the mortality occurs shortly after emergence. Territories are most likely formed upon emergence. Fry that have less desirable territories, or no territories at all, are less likely to survive. It has not been shown that predation by either brook trout or other vertebrates accounts for loss of fry. It was demonstrated that brook trout fry are relatively long-lived in the face of starvation, but the possibility exists that a rather short period of starvation may deter them from feeding effectively or assimilating the food that they do obtain. Death rate of trout fry from starvation increases with a rise in water temperature. Groundwater levels probably act as a physical factor of the environment to regulate the number of trout in the stream.

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Chitty in 1967 stated "The trouble is that animals die for all sorts of reasons (including starvation) and that anyone who works at it hard enough can find a correlation of some sort to support his views, whatever they happen to be." My objective in the following is to review some of the literature and present data from my own experiments and experiences in an effort to explain some of the reasons why brook trout die during their first year of life. I particularly want to discuss starvation as a population control mechanism and among other things I will consider correlations of groundwater levels with abundance of young-of-the-year brook trout.

Magnitude and periodicity of mortality

Survival in brook trout from egg to fingerling stage has been well documented to be about 2 to 8% (Smith, 1947; Cooper, 1953; McFadden, 1961; Shetter, 1961; McFadden, Alexander, and Shetter,

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1967). Mortality during this early stage of life is much greater than in subsequent years and appears to be compensatory or density dependent; that is, when the number of potential eggs to be spawned is large, mortality of fry is large (McFadden, 1961; McFadden, et al., 1967). In Hunt Creek, Michigan, compensatory mortality extends into the second year of life but it is not nearly as great as during the first year (McFadden, et al., 1967). In both Hunt Creek and Lawrence Creek, Wisconsin, compensatory mortality apparently does not extend into the later years. Ricker's (1954) assumption that most if not all of the compensatory mortality occurs during the early stages of life of fish seems to be true in these brook trout populations for which several years of data are available (McFadden, 1961; McFadden, et al., 1967). Le Cren's (1962) experiments with fry of brown trout (Salmo trutta) in enclosures in a beck reinforce the field analyses made on brook trout which indicate density dependent survival of fry. Support for the belief of density dependence of fry survival is provided also by the observation in other brook trout populations that no relationship exists between number of spawners and number of progeny surviving till fall (Latta, 1965; Shetter and Alexander, 1966).

In the experimental sections of the Pigeon River, Michigan (Latta, 1965), spawning reaches a peak in late October or early November. Emergence occurs in the latter half of March. Assuming high survival in the redds, most of the mortality of the fry takes place between late March and late June (Latta, 1962). Hunt's (1966) population figures for brook trout indicate the same pattern of mortality for the same 3 months in Lawrence Creek. A similar pattern exists for brown trout fry (Allen, 1951; Le Cren, 1965).

Although survival in the redd for brook trout is usually considered to be about 90%, studies published to date have not been definitive (White, 1930; Hazzard, 1932; Brasch, 1949; McFadden, 1961). As McFadden (1961) pointed out, with the exception of Brasch's (1949) preliminary work, no estimates are available for brook trout of mortality occurring as the fry emerge from the gravel.

Although high density in the spawning area in some salmonids can lead to loss of eggs through superimposition of the redds and retention of eggs in the females (Johnson, 1965), these do not appear to be problems in the brook trout. Shetter (1961), in a spawning experiment in the diversions of Hunt Creek, found only 6 of 27 females retaining eggs and the number withheld was only 67 eggs for 3 females. However each female had at least 435 square feet of stream in which to spawn.

Factors affecting survival of fry during the first summer of life

For the brook trout I believe the time and magnitude of the compensatory mortality that controls population size have been established. The next problem is to determine the causes of mortality and how they function. Typically it is suggested that mortality is caused by disease, predation or lack of food. So little is known about disease among wild fish of any size (Davis, 1947) that I will not comment on it as a factor in mortality of trout fry.

Behavior

Territorial behavior apparently plays an important role in the regulation of population size in salmonids (Chapman, 1966). Brook trout form territories at an early age (Newman, 1956; Keenleyside, 1962). Arne J. Salli and Arthur D. Hasler (in an abstract of a paper given at the American Fisheries Society meeting, Atlantic City, New Jersey, September 1964) reported brook trout fry established territories in the Brule River, Wisconsin, shortly after emergence. Kalleberg (1958) found that brown trout upon emergence started to feed and then immediately developed aggressive behavior. The aggressiveness led to the establishment of territories. Defense of the territories was directly related to the velocity of the current and the degree of visual isolation. Aggressiveness increased with an increase in available food, and territories were abandoned at high densities of fry. Although Kalleberg (1958) and Keenleyside and Yamamota (1962) stated that territories of salmonid fry are established primarily for feeding, Chapman (1966) concluded that competition for space may be as important as competition for food in the establishment of territories. Keenleyside (1962) observed some young brook trout in the Miramichi River defending territories on shallow rapids and others in pools and backwaters in groups resembling schools. A study of the behavior of newly emerged brook trout is needed.

Predation

The establishment of territories leads to a more uniform distribution of trout fry and presumably to a more efficient utilization of the food supply and to better survival from predation and disease. Territorial behavior also forces some individuals, undoubtedly the smaller fry, into areas of the stream that are less desirable for food and survival. These individuals could be eaten by brook trout or other predators; however, Shetter (1961) pointed out, in his experiments in the diversions, that there was no relationship between "numbers of extraneous trout present (0 to 5) and percentage survival of the fry (4.5-31.7)." Mean survival in the diversions was 10.8%, while in Hunt Creek proper, where large numbers of resident brook trout were present, mean survival was 3.7%, only slightly less than in the absence of potential predators. Shetter also suggested that predation from birds and mammals at the diversions was reduced because of human activities there. Gaylord R. Alexander (personal communication) has found no evidence that older brook trout prey upon newly emerged fry in Hunt Creek. Le Cren (1965) expressed doubt that other species of fish are important predators on stream salmonids. Lowry (1966), although he did not believe that he had sampled at the appropriate time and place, found little predation by cutthroat trout (*Salmo c. clarki*) on newly emerged coho fry (*Oncorhynchus kisutch*).

Starvation

Starvation should be considered as a mortality factor in brook trout fry. Previous studies of starvation of salmonids as a cause of mortality or as a factor in weight loss have indicated that (1) mortality and weight loss increased as temperature increased (Kawajiri, 1928; Lawrence, 1941; Phillips, Lovelace, Brockway, and Balzer, 1953), and (2) the smaller fish (3.5-inch group) had a greater mortality than the larger fish (5.5- and 7.5-inch groups) (Adelman, Bingham, and Maatch, 1955). Starved brook trout are remarkably long-lived. The starvation experiment of Adelman, et al. (1955) lasted for 7 months with a loss of 70% for the 3.5-inch group, 25% for the 5.5-inch group and 10% for the 7.5-inch group of trout. Phillips, et al. (1953) had a 16.9% loss of fish in 14 weeks for the brook trout held at 54 F and virtually no loss for those held at 47 F.

Experiments were conducted in 1962, 1964 and 1965 at the Pigeon River Research Station to measure mortality from starvation, in relation to temperature, of newly emerged brook trout fry. Wild trout were used to eliminate the influence of domestication (Vincent, 1960). Fry were collected from the Pigeon River in March as soon as they appeared along the margins of the stream. In all years the fry at time of collection were about 23 mm long (Table 1). Fry were held in 5-gallon aquaria (8 x 10 x 14 inches). In each experiment two aquaria were designated as experimentals and two as controls. Twenty-five fry were placed in each aquarium. A stream of well water (about 100 ml per minute) was sprayed into each tank at an angle of about 45°. Dissolved oxygen in the aquaria varied from about 6 to 8 ppm. The control fish were fed a liver-cereal ration regularly, while the experimental fish were completely starved. The fry were held at mean temperature regimes of 40.2, 42.4, 44.7 and 50.5 F. A summary of the total number of deaths from starvation at the four temperatures is given in Table 2.

In the control aquaria held at the temperature of 40.2 F, 16 of the 50 fry died. The cause of this unexpected mortality was unknown. It occurred suddenly and before the bulk of the starvation mortality in the experimental aquaria. Mortality was also slightly greater than expected in the control aquaria held at 50.5 F. Apparently these deaths were caused by a lack of sufficient food, at the rather high metabolic rate of the fry, for the mortality stopped with an increase in the daily ration.

Survival curves for the experimental fish held at the four temperatures are presented in Figures 1 and 2. The variations in mortality between paired aquaria for each temperature were slight. The estimated number of days for 25, 50 and 75% mortality from starvation of brook trout fry held at the four temperatures is given in Table 3 and presented graphically in Figure 3.

Unfortunately the experimental equipment did not permit holding the temperatures as constant as would have been desirable. In the experiment at 40.2 F the temperature towards the end of the experiment climbed slowly from slightly below 40 to 50 F. Undoubtedly this temperature increase precipitated the mortality. To a lesser extent the 42.4 temperature regime did the same. It rose from 41 to 46 F. If the temperatures had been held constant the slope of the curve in Figure 3 at the lower temperatures would have been increased.

Kawajiri (1928) considered death from starvation for fry of sockeye salmon (Oncorhynchus nerka) and rainbow trout (Salmo gairdneri). He measured total mortality, in days from time of hatching, for temperatures that ranged from 2.5 to 16.4 C. Although his data are not directly comparable to mine, the general curvilinear relationship that he found between temperature and number of days to death from starvation is similar to that shown in Figure 3.

Usually brook trout fry upon emergence in the Pigeon River are found along the edges of the stream in areas influenced by groundwater. Spawning also occurs in these areas (Benson, 1953). The differences in water temperatures between the edge influenced by groundwater flow and the middle of the stream at the time of emergence is illustrated in Figure 4. The mean water temperature for the edge in 1965 was about 40 F. At 40 F it would require about 70 days for 50% mortality of brook trout fry (Fig. 3). However a slight increase in the water temperature to say 44 F, the stream temperature in late April, would reduce the mortality time for 50% of the fry to 34 days.

The fry were not subjected to any amount of current in the aquaria. The stream of water entering each aquarium caused only a slight rotation of the water. Under stream flow conditions, the physical environment would be much more harsh and I would expect starved fry to die sooner than they did in the aquaria. Le Cren (1965) judged that the brown trout fry without territories, in his experiments in cages and screened portions of becks, were dying from starvation between the 20th and 40th days after start of feeding.

Ivlev (1961) showed that the effects of unfavorable environmental conditions, both physical and biological, were intensified in relation to starvation. He used the fry of several species of Asiatic fishes as test animals. For physical factors, he tested the effects of swimming fatigue (current), phenol, salinity, pH and oxygen concentration in relation to starvation, and for biological factors he investigated parasitism, incidence of fungus infection and the starved fish as a prey and as a predator. He concluded that "complete and partial starvation are ecologically synonymous and differ only in intensity." Barrow (1955) also showed that some species of fish were able to reduce infection from trypanosomes when they were socially dominant and obtained the most food.

Toetz (1966) found that 50% of bluegill fry (*Lepomis macrochirus*) died of starvation at 8.5 days after fertilization or about 6 days after hatching (water temperature 23.5 C). The critical period for survival was between the beginning of feeding at 6.4 days and starvation at 8.5 days.

John and Hasler (1956) found cisco larvae (*Leucichthys artedi*) had 50% mortality in about 25 days from the time of hatching at temperatures that started at 4 C and rose to 11 C during the experiment. They state that, "Although 100 per cent of the larvae survived through 22 days of starvation, after 18 days some had apparently become too weakened to take advantage of the food made available to them." At temperatures between 3 and 4 C the larvae withstood 30 some days of starvation. They did not believe that cisco larvae could starve to death in Lake Mendota.

The decrease with starvation of ability to take food (or assimilate food once it has been obtained) probably also occurs in brook trout. Adelman, et al. (1955) after starving the 3.5- to 7.5-inch brook trout for 7 months, divided the fish into a "demand-feed" group and a "slow-feed" group. All of the fish in the "demand-feed" group died whereas none died in the other group. Atkins (1906) placed four groups of brook trout fry of 1,000 each in 10-foot hatchery troughs and starved them for 5, 9, 14 and 19 days respectively, before feeding. The experiment started May 23 and lasted through September. Mortality occurred in proportion to the number of days the fry were starved. For the 5 days of starvation, mortality was 9.8%, for 9 days--11.8%, for 14 days--56.2% and for 19 days--79.0%. Most of the deaths occurred in June immediately after feeding started. In the following months mortality was slight and not in proportion to days of starvation. Water temperatures or volumes of flow in the troughs were not given. Judging from my data 19 days is not sufficient time for death to occur directly from starvation (Fig. 3). Atkins' experiment suggests that after a rather short period of starvation not all brook trout fry are capable of utilizing food.

Groundwater

In the Pigeon River I found a significant correlation between abundance of young-of-the-year brook trout and groundwater levels (Latta, 1965). Large numbers of young-of-the-year brook trout were present during years of high groundwater levels. Apparently this relationship is not true for Lawrence Creek or Hunt Creek. In 1965, Robert L. Hunt wrote that such a relationship did not exist in Lawrence Creek (personal correspondence). For Hunt Creek, I took the population figures for 0-age-group brook trout provided in McFadden, et al. (1967) and compared them with the groundwater levels for well No. 21-1 in T. 29N., R. 3E., Montmorency County, Michigan as measured by U. S. Geological Survey, Lansing, Michigan. This well is not in the watershed of Hunt Creek but is approximately a mile from the stream. The correlation coefficient (r) for these data for the years 1949-62 was only -0.13.

In both Hunt Creek and Lawrence Creek the numbers of 0-age-group brook trout have varied less than in the Pigeon River (McFadden, 1961; Latta, 1965; Hunt, 1966; McFadden, et al., 1967). Apparently numbers of young-of-the-year trout fluctuate less in the headwaters than in the lower reaches of trout streams. In the Pigeon River the groundwater flow (as a percentage of the total volume of the stream) is greater in the headwaters (Benson, 1953). In the 6 miles of experimental water of the Pigeon River annual fluctuations in numbers of 0-age-group trout are less as you go upstream.

How groundwater levels influence survival of brook trout fry is not known. Undoubtedly in years of high groundwater levels, the area along the edge of the stream which the fry occupy immediately after emergence is increased in size. Water temperatures would be more moderate (Benson, 1953). Ball and Hooper (1963) indicated that the phosphorus content of the West Branch of the Sturgeon River (a neighboring stream of the Pigeon River) increased somewhat with rains. Although there is no significant transport of phosphorus through percolating groundwaters (Taylor, 1967), years of increased groundwater are identical with years of high precipitation in northern Michigan (Latta, 1965). Perhaps during years of high rainfall (and groundwater) nutrient flow to the stream is increased. Groundwater can be characterized as a physical factor of the environment probably influencing population size in a non-compensatory way as opposed to the biological factors of disease, starvation and predation which act in a compensatory manner.

Summary

It appears that compensatory mortality caused by disease, predation or starvation during the first year of life determines the population size in brook trout populations. Although little is known about losses during emergence from the redds, it is presumed that most of the mortality occurs shortly after emergence. Territories are most likely formed upon emergence. A comprehensive behavioral study of territoriality in brook trout fry is needed. Certainly those fry that have less desirable territories, or no territories at all, are less likely to survive. It has not been shown that predation either by other brook trout or by other vertebrates accounts for the loss of fry. Although it has been demonstrated that brook trout are relatively long-lived in the face of starvation, the possibility exists that a rather short period of starvation may deter them from feeding effectively or assimilating the food that they do obtain. Starvation undoubtedly lowers their resistance to biological and physical stresses of the environment such as predation or increases in flow of the stream. Groundwater levels act as a physical factor of the environment to regulate the carrying capacity of the stream.

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INSTITUTE FOR FISHERIES RESEARCH

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Report approved by G. P. Cooper

Typed by M. S. McClure

Table 1.--Total length and weight of brook trout fry captured at various times for use in starvation experiments

Collection dates[a]	Number of fry	Mean total length (mm)	Standard deviation	Mean weight[b] (g)	Water temperature[c] (F)
March 16, 20 1962	13	23.5	1.3	0.072	37
March 10-12, 16, 1964	25	23.4	2.0	0.072	37
March 8-10, 11, 1965	51	23.3	1.8	0.078	35

[a] Collections for the experiments were made on the earlier dates; samples for total length and weight measurements were taken on the last date.

[b] Total weight of fry divided by number of fry.

[c] Water temperature was measured in mid-stream.

Table 2.--Number of deaths from starvation of brook trout fry held at four temperatures

Year		Mean water temperature[a] (F)	Experimental fish		Control fish		Total days of experiment
1962	Dead	42.4 ± 0.6	22[b]	24	3	1	49
	Alive		2	1	22	24	
1964	Dead	44.7 ± 0.4	23	23	2	6	37
	Alive		2	2	23	19	
1965	Dead	40.2 ± 1.2	25	20	5	11[b]	75
	Alive		0	5	20	12	
	Dead	50.5 ± 0.6	22	20	6[b]	8[b]	31
	Alive		3	5	18	16	

[a] Confidence limits at the 95% level; an analysis of variance indicated the mean temperatures were significantly different at the 99.5% level.

[b] Totals of less than 25 resulted from losses of fry from aquaria during feeding and cleaning.

Table 3.--Estimated number of days for 25, 50 and 75% mortality from starvation of brook trout fry held at four temperatures

Mean water temperature (F)	Per cent mortality		
	25	50	75
40.2	63.0	67.5	71.0
42.4	40.5	44.5	47.0
44.7	27.0	31.0	34.5
50.5	25.5	27.5	29.5

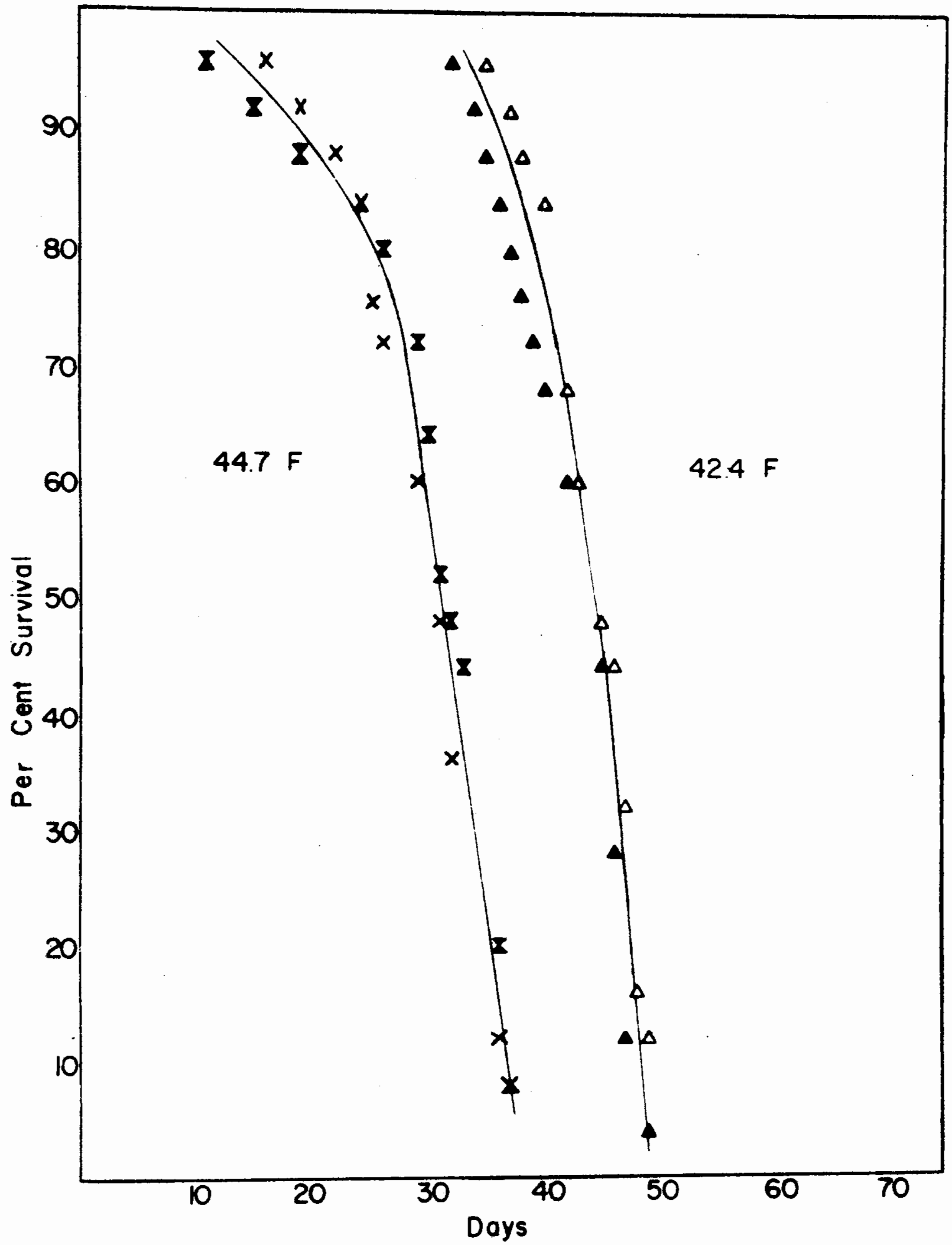

Figure 1. --Survival curves for newly emerged brook trout fry starved at mean temperatures of 42.4 F and 44.7 F in 1962 and 1964, respectively. Open and shaded symbols distinguish the two aquaria in each experiment.

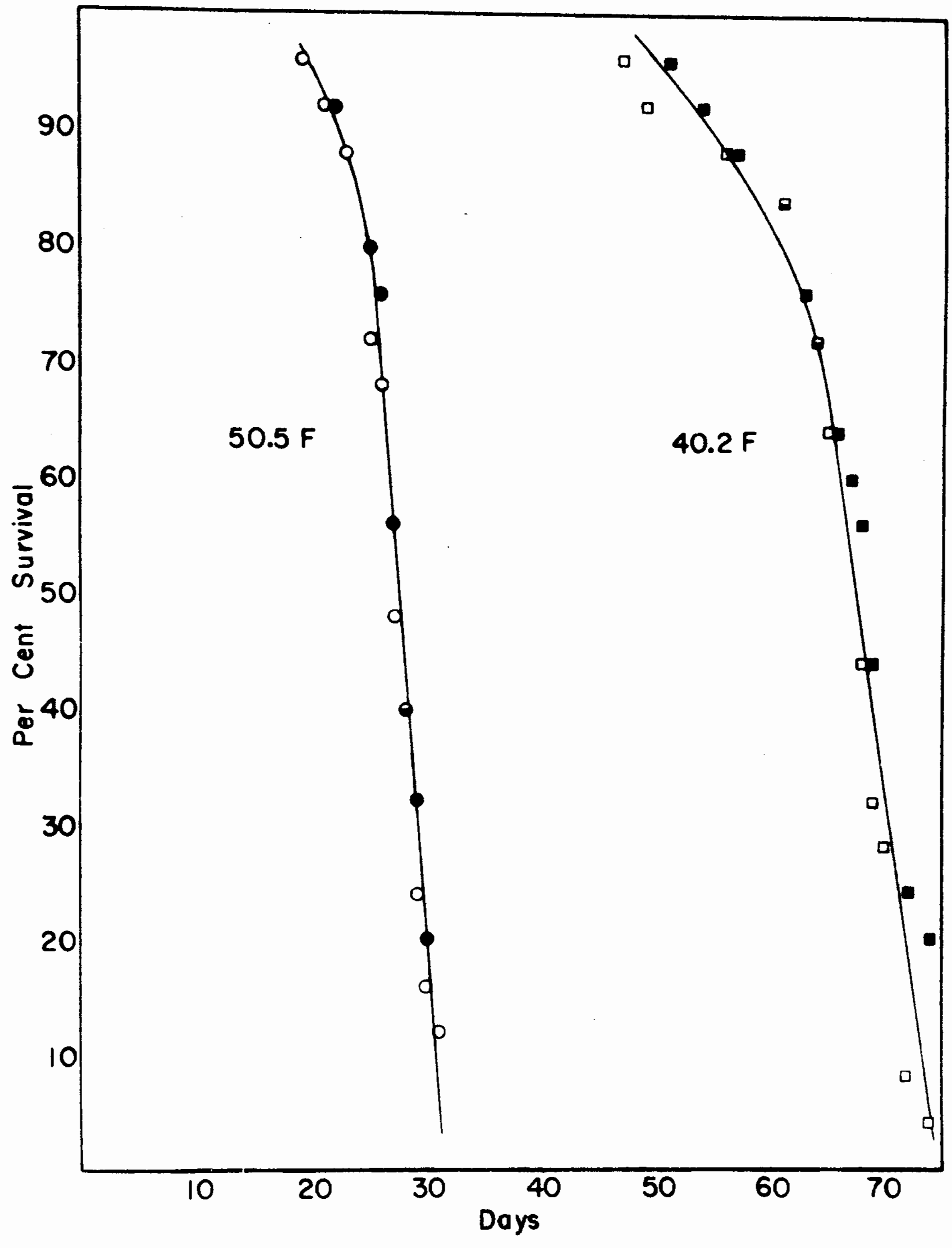

Figure 2.--Survival curves for newly emerged trout fry starved at mean temperatures of 40.2 F and 50.5 F in 1965. Open and shaded symbols distinguish the two aquaria in each experiment.

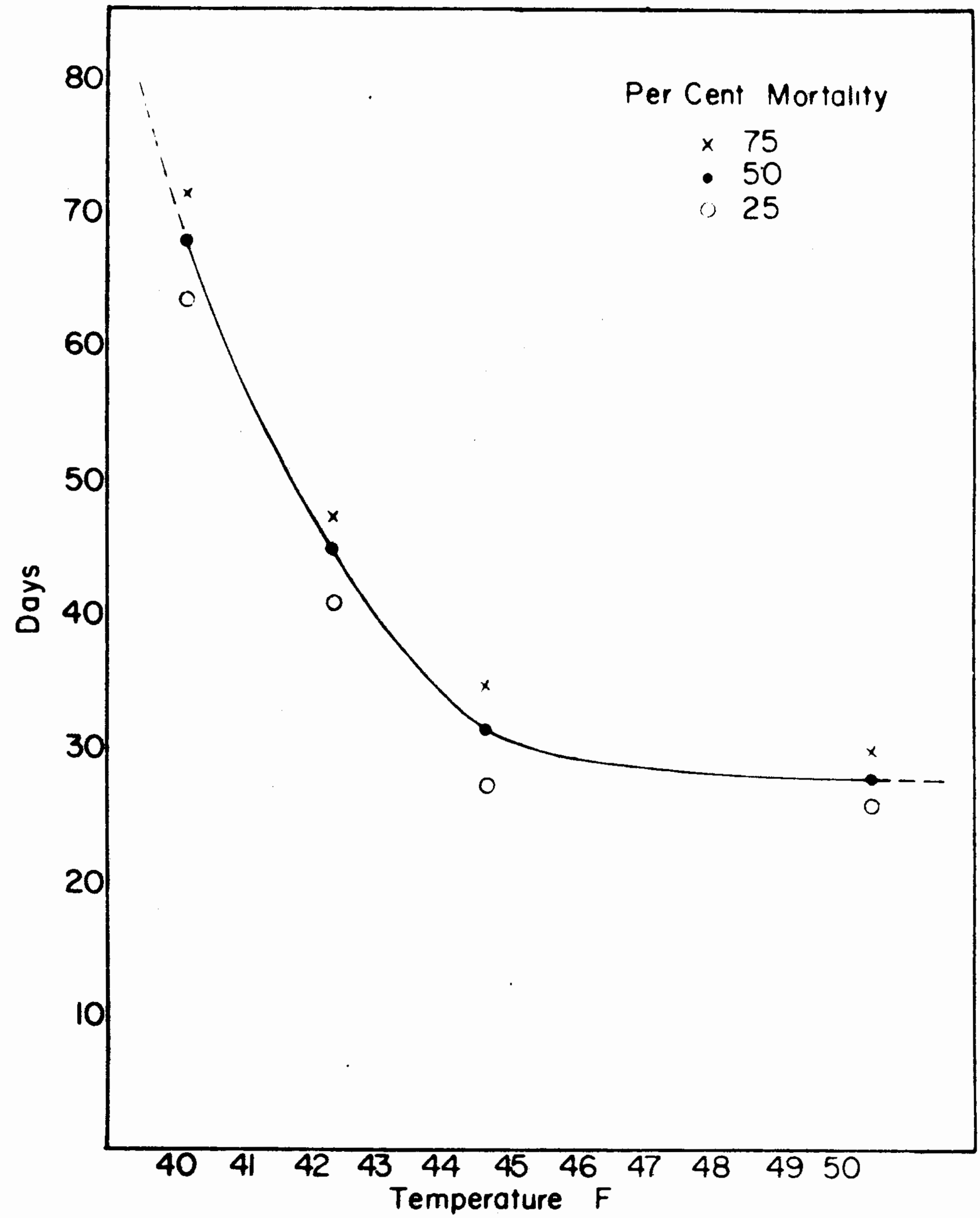

Figure 3. --Relationship of number of days for 50% mortality at different temperatures for starved brook trout fry. The 25 and 75% levels of mortality are indicated also.

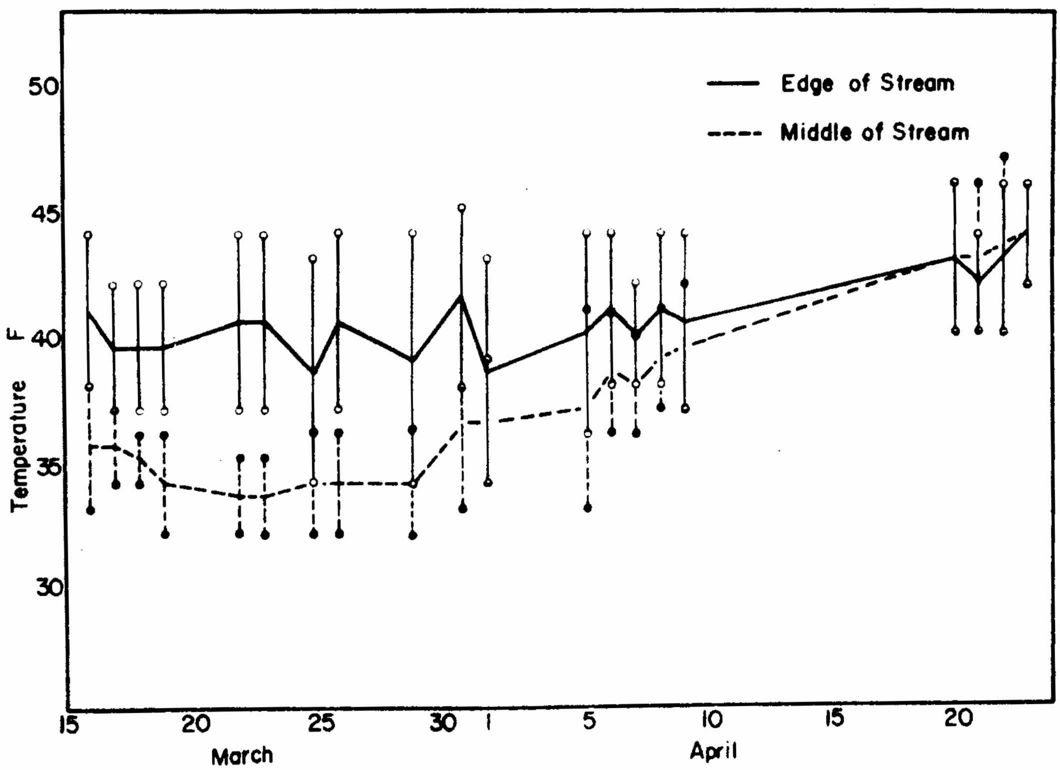

Figure 4.--Mean water temperatures for the edge and middle of an area influenced by groundwater seepage in the Pigeon River, 1965. Vertical lines indicate the daily maximum and minimum temperatures.