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Growth, Mortality Rates, and Standing Crops of Trout in New York Farm Ponds

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Contents

Growth, Mortality Rates, and Standing Crops of Trout in New York Farm Ponds[1]

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The primary objective of this paper is to present information on growth, mortality, population density, and biomass (standing crop) of hatchery trout stocked in central New York farm ponds. Interactions of the various population processes with each other and with environmental factors are examined. Findings demonstrate the pronounced variability in growth and mortality among individual ponds, the need for more information on basic fish population mechanisms, and the usefulness of small earthen impoundments for obtaining some of this information.

A 3-year investigation of trout in New York farm ponds made by Saila (1952) provided valuable preliminary information and a basis for the present study. The data considered here were obtained from a series of experiments conducted in 70 farm ponds from 1952 through 1958. Management recommendations for the estimated 4000 New York farm ponds currently stocked with trout have already been published (Eipper, 1960; Eipper and Regier, 1962). These recommendations are based on findings of the present study supplemented, where appropriate, by information from Saila (*op. cit.*).

Characteristics of the Study Area and Ponds

All but 3 of the 70 farm ponds that were used are located within a 20-mile radius of Ithaca, New York. This area is characterized by rolling topography and agricultural lands of diverse soil types but generally low to moderate fertility. Half of the ponds were at elevations between 800 and 1200 feet (table 1). Physiographic features and soil associations of this area are given by Cline (1955); the climate is described by Mordoff (1949). Nine of the ponds were on Cornell University lands; the rest were privately owned.

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[1] A contribution of Federal Aid in Fish Restoration Project F-17-R and Hatch Project 80.

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Table 1. **Distribution of the 70 experimental farm ponds in 4 categories of elevation (ft) above mean sea level**

Elevation (ft)	Number of ponds
400–799	8
800–1199	26
1200–1599	23
1600–1999	9

The term "farm pond" as used here denotes a small impoundment restricted to a basin scooped out of relatively impervious subsoil. Usually the basin is made on gently sloping ground, in which case an earthen dyke is pushed up on the downhill side to increase water volume. All of the experimental ponds were constructed after 1943, most of them with assistance from the Soil Conservation Service, USDA. Virtually all the ponds were of similar morphometry, as standardized in Soil Conservation Service specifications described and figured, for example, by Winkelblech (1955). Surface area and maximum depth statistics of experimental ponds are given in table 2. Half of the ponds had surface areas of 0.2 to 0.4 acres; 70 percent between 0.2 and 0.7 acres, inclusive. The average depth (volume divided by surface area) of most ponds was about one-half the maximum depth. Area and depth statistics of experimental ponds closely approximated those for all farm ponds in New York State.

Table 2. **Surface areas and maximum depths of the 70 farm ponds used in trout population studies**

Variable	Mean	Mode	Range
Surface acres	0.42	0.2	0.1–1.8
Maximum depth (ft)	7.63	8.0	5.0–14.0

Forney's (1957) summary of physical–chemical data from 48 central New York farm ponds (including 12 of the trout ponds) shows the large variations between seasons and/or between ponds in temperature, dissolved oxygen, pH, total alkalinity, total dissolved solids, nitrogen, and phosphorus that may be expected in these waters.

From records of physical–chemical determinations made at various times in various groups of the trout ponds, it seems likely that all of them fall within the ranges given by Forney. Total alkalinities in 15 of the trout ponds ranged from 20 to 160 ppm. Dissolved oxygen in bottom waters seldom was less than 4 ppm at any season, except in the few ponds that were heavily fertilized and/or those in which unusually large amounts of vegetation decomposed under a prolonged ice cover.

Ponds of this area are usually ice-covered from December through March, and snow-covered for 2 or 3 of these months. In warmer summers, surface and bottom water temperatures attain maxima of around 86° and 80° F, respectively, for short periods in many of the ponds lacking a permanent spring-water supply. Thermal stratification is commonplace in New York farm ponds, but seldom persists for more than 2 weeks.

Many kinds of submerged, floating, and emergent aquatic plants are found in these ponds, and invasion usually begins 1 or 2 years after the pond has filled. Filamentous algae also are common. Phytoplankton pulses are relatively infrequent and seem to bear little direct relationship to fertilization practices, except that they occur more frequently in ponds that receive inflow from heavily manured watersheds. Very few of the experimental trout ponds were ever fertilized.

Immature forms of chironomids and odonates are conspicuous insect components of bottom fauna in most central New York farm ponds, and adult notonectids are often abundant. Various snails, such as *Physa*, *Lymnaea*, and *Planorbis*, are common in many of the ponds. Besides fish, the most abundant vertebrates are frogs and salamanders. Substantial poundages of tadpoles and newts (*Notophthalmus viridescens*) have been seined from these ponds in some fish population inventories.

Design and Chronology of Experiments

An immediate objective of the experiments described here was to determine management techniques that would produce optimum yields of trout in New York farm ponds. The basic experimental approach employed was to formulate (on the basis of previous findings) an hypothesis — or sets of alternative hypotheses — about desirable trout management techniques, to initiate tests of these techniques in series of ponds, and to evaluate results by periodic inventories of the number and size of fish remaining in each pond. The principal categories of investigation were as follows:

- Relative merits of brook trout, *Salvelinus fontinalis* (Mitchill), and rainbow trout, *Salmo gairdneri* Richardson. (Saila, 1952, had already demonstrated that brown trout, *Salmo trutta* Linnaeus, are unsuitable for New York farm ponds because of their extremely low vulnerability to angling in these waters.)
- Relative merits of spring fingerling (age 0) and fall fingerling (age 0+) trout for farm pond stocking.
- Optimum numbers of spring fingerling and fall fingerling trout to stock, per acre of pond surface, and the effect of species and/or pond size on these determinations.
- Farm pond survival of late- or non-maturing salmonids, relative to that of standard plantings of hatchery brook or rainbow trout. These tests were initiated because of the possibility that natural mortality rate of farm pond trout might increase after the attainment of sexual maturity. Brook × brown trout and brook × lake trout, *Salvelinus namaycush* (Walbaum), hybrids were used in these tests, and also a late-maturing strain of wild brook trout from Cranberry Lake, New York.
- Extension of Saila's (1952) observations on trout reproduction in farm ponds and the utility of artificial spawning areas. Tests of devices for incubating trout eggs in ponds.

In addition to tests falling in the above experimental categories, various plantings of miscellaneous strains, species, and/or ages of salmonids were made in single or small groups of ponds on various occasions during the 8-year study. Such plantings were made when unexpected opportunities presented themselves, and were outside the framework of any planned experimental design.

Table 3. **Chronological summary of data on salmonid plantings in farm ponds, 1952 through 1957**

Year	Date	Species*	Age†	No./acre stocked	No. of ponds	Mean total length (in.)	Hatchery source‡	Remarks
1952	May 23	Brook	0	400 800	8 8	2.1	Cortland	
	May 27	Rainbow	0	2,000	1	. . .	Bath	Unfed fry; wild parents
	Oct. 14	Brook	0+	300 600	4 4	4.4	Cortland	
	Oct. 16	Rainbow	0+	300 600	4 4	6.9	Cortland	
	Oct. 24	Brook Brook	0+ 0+	175 175	4§	3.7 3.3	Cortland Catskill	Domestic vs. late-maturing (Cranberry L., N.Y.) strain
	Oct. 13	Rainbow	0+	600	1	6.5	Cortland	Odd lots stocked in 4 individual ponds
	Oct.–Dec.	Brook	0+	250–350	3	3.7–6.7	Cortland	
1953	May 28	Brook	0	400 800	3 3	2.5	Cortland	
	May 15	Brown × brook	0	375	1	1.6	Cornell	Wild parental stock
	" "	Brook × brown	0	420	2	1.7	"	" " "
	" "	Brook × lake	0	450	2	1.7	"	" " "
	" "	Lake × brook	0	450	3	1.6	"	" " "
	May 22	Lake	0	300	2	. . .	"	" " "
	May 26	Brook Brook × brown	0 0	230 230	1§	2.5 2.5	Cortland Bellefonte	Wild parental stock
	June 3	Brook	0	750	1	2.6	. . . . . .	Wild; seined from stream
	Nov. 3	Brook	0+	400 500	3 3	5.7	Elbridge	
	Nov. 17	Rainbow	0+	110	1	6.4	Cortland	
1954	May 15	Brook	0	400 800	6 6	1.9	Elbridge	
	May 26	Brook × lake	0	450	2	1.5	Cornell	Wild parental stock
	Oct. 5	Brook	0+	300 600	2 2	5.4	Elbridge	

Table 3. (*continued*)

Year	Date	Species*	Age†	No./acre stocked	No. of ponds	Mean total length (in.)	Hatchery source‡	Remarks
1954 (*con't*)	Oct. 5	Rainbow	0+	300 600	3 3	4.1	Elbridge	
	Oct. 20	Brook × brown	0+	400	6	4.3	Bellefonte	
	Oct. 20	Brook × brown Brook Rainbow	0+ 0+ 0+	100 100 100	1§	4.3 5.4 4.1	Bellefonte Elbridge	Domestic parental stock
	Nov. 5	Brook	0+	400	2	7.0	Cortland	
1955	May 1	Brook Brown	I I	100 80	1§	... ...	Cortland Cortland	
	May 2	Brook × brown	0	300	1	1.8	Cornell	
	May 15	Kokanee	0	800	5	ca. 1	Cornell	*O. nerka kennerleyi* eggs from Flathead Lake, Montana
	Sept. 28	Brook × brown	I+	150	7	13.4	Bellefonte	Domestic parental stock
	Oct. 12	Rainbow	0+	250 300 400	2 6 5	6.5	Cortland	
	Oct. 21	Brook	0+	50 100	2 1	4.5	Cortland	
1956	May	Landlocked salmon	0	3,000	2	ca. 2	Cornell	*Salmo salar sebago*
	May	Brook	0	1,200	1	ca. 2	Cornell	
	Sept. 19	Rainbow	0+	300	9	6.9	Cortland	
1957	June 7	Brook	0	1,000	4	2.0	Cornell	

* Hybrid designations: (paternal species) × (maternal species).

† Age 0: hatched approximately 3 months previous; age 0+: hatched approximately 9 months previous.

‡ Cortland: National Fish Hatchery, U. S. Fish and Wildlife Service, Cortland, New York.
Elbridge: National Fish Hatchery, U. S. Fish and Wildlife Service, Elbridge, New York.
Bath Hatchery: New York State Conservation Department, Bath, New York.
Catskill Hatchery: New York State Conservation Department, Livingston Manor, New York.
Cornell: Fishery Laboratory, Department of Conservation, Cornell University, Ithaca, New York.
Bellefonte: Benner Spring Research Station, Pennsylvania Fish Commission, Bellefonte, Pennsylvania.

§ Equal numbers of each group stocked in each pond. Cortland fish (domestic) identified, when necessary, by removing adipose fin.

When simultaneous tests of 2 stocking rates were initiated, equal numbers of ponds were usually stocked at each rate, and ponds in the 2 stocking categories were matched as closely as possible with regard to surface acreage and water supply (spring vs. runoff water).

Table 3 gives a chronological summary of the various experimental farm pond plantings of salmonids in the years 1952 through 1957, inclusive, with pertinent data on the fish and ponds involved in each test.

Although it was planned to employ stock from the Cortland hatchery exclusively in all farm pond experiments with brook and rainbow trout, it proved necessary to obtain most of the stock for the fall 1953, and spring and fall 1954, plantings of these species from the Elbridge hatchery.[2] Consequently, possible effects of hatchery origin were confounded with effects of calendar year in the analyses of growth and mortality data.

Procedures

Selection of farm ponds for trout experiments was governed chiefly by 4 criteria:

(1) ***Proximity to Ithaca.*** The replication of experiments required by the great variability between ponds made it necessary to restrict geographic scope of the research.

(2) ***Pond size.*** No ponds of less than 0.1 surface acre, and only 10 less than 0.2 acre, were used for experiments. Besides being atypical in size, very small ponds are unsuitable for many experiments because slight numerical changes in their small fish populations can produce proportional changes that may be exaggerated in comparison with those made by similar numerical changes in larger populations. Surface acreages of experimental ponds were determined by plane table survey in the majority of cases. In the rest, acreages determined by the Soil Conservation Service at construction time were used, with dimensional measurements to check the accuracy of these determinations.

(3) ***Pond construction features.*** Features that negated or reduced the experimental value of farm ponds included leaks, extensive shoal areas (which fostered heavy growths of aquatic plants and thus impeded seining), and bottom obstructions such as boulders and submerged pipes.

(4) ***Characteristics of pond ownership and use.*** Experiments were confined to those ponds whose owners cooperated actively in maintaining records of angling, weed control, fertilization, and other management procedures, and to ponds whose uses did not endanger the research.

The methods used to make chemical determinations in the experimental ponds have been described by Forney (1957). Temperatures

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[2] Affiliations and locations of the hatcheries are given in footnote ‡, table 3.

were measured with a thermistor thermometer accurate to 0.5° F.

Stocking

Fingerling trout were transported from the hatchery to experimental ponds in tanks supplied with oxygen liberators. As shown in table 3, age 0 trout were stocked before June 8 (usually May 15 or earlier), age 0+ trout after September 18 (usually after October 1), when surface temperatures of ponds were 65° F or below. Trout for each pond were counted out individually into buckets, using a hand tally counter and small dip net. No fish evidenced distress before or after any of the plantings. A subsequent section (*Reliability of Population Estimates*) presents quantitative evidence that mortality during the first month following stocking was slight.

Fishing

Angling for age I and older trout in experimental ponds was conducted by pond owners and their friends. Trout pond owners were enthusiastic and cooperative, and virtually all of them in all years maintained records of catch, number of anglers, and hours fished on each fishing day. Although poaching occurred on several occasions in 3 remotely situated University ponds, it was apparently negligible in the rest, each of which was located near the owner's or supervisor's house.

Fertilization; Weed Control

The few owners who occasionally fertilized their trout ponds (using 5–10–5 or other inorganic fertilizers) provided records of the applications, as did those who applied aquatic herbicides. Owners of experimental trout ponds were advised not to fertilize, and usually aquatic weed growths heavy enough to obstruct seining were treated with herbicides by research personnel in late August or early September. Copper sulfate was used to control unbranched filamentous algae and sodium arsenite for higher aquatic plants, as outlined by Eipper and Brumsted (1957). The available evidence indicates that these applications did not affect either growth or mortality of the trout (Eipper, 1959), although critical experiments designed specifically to measure such effects were not conducted.

Inventory

Experimental ponds were inventoried in spring (April–May) and/or fall (October–November). Surface water temperatures were usually well below 65° F when ponds were inventoried; no inventories were made when surface temperatures exceeded 68° F.

The net commonly used to inventory trout pond populations was a seine 150 feet long, 8 feet deep in the center and tapered, on the bottom only, to 5 feet deep at each end. A bag, 8 feet wide by 8 feet high, was located in the center of the seine, tapered to a rounded point and hung to trail 10 feet long when the seine was fished. The bag was made of ½-inch mesh; the rest of the seine was ¾-inch mesh (bar measure).[3] For populations of

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[3] Bar (square) measure will be used to denote all mesh sizes given in this paper.

age 0+ trout, which were sometimes gilled in the above net, a 75-foot seine made entirely of ¼-inch mesh was used. This seine was 8 feet deep in the center, tapered on the bottom to 4 feet deep at each end, with an 8 × 8 × 8-foot bag set in the center. Both seines were weighted sufficiently to fish the bottom regardless of water depth (although this seldom exceeded seine height appreciably), and either seine was normally operated by 2 men. Cotton mesh was used until 1956; nylon mesh was used exclusively thereafter. Usually all seine hauls were made starting at the deep (dyke) side of the pond and ending on the opposite side, where the slope was most gradual.

Standard inventory procedure involved seining the pond twice for a Petersen population estimate. All trout obtained in the first haul were placed in live cars, then temporarily marked by removing a quarter-inch corner of the dorsal lobe of the caudal fin, and immediately distributed fairly uniformly around the pond perimeter by two men with buckets. In ponds larger than 1 surface acre, marked fish usually were distributed by boat. From 20 minutes to 3 weeks after the marked fish were released, a second "recapture" seine haul was made, identical to the first. Trout were easily seined in these ponds, and ordinarily only 2 seine hauls were required for population estimates that were considered reliable. Sample sizes and accuracy of population estimates are discussed in the next section.

Two criteria were used jointly in the field to judge the adequacy of sample sizes:

- That marked fish comprise at least one-third of the total catch in the second (recapture) seine haul (an indication that at least one-third of the total population had been captured and marked in the first haul).[4] If this requirement was not met, the unmarked fish in that haul were marked, all fish were released, and another recapture haul was made within 2 days.
- That at least one-third of the fish marked and released after the first haul be recaptured in the second haul (an indication that at least one-third of the total population was represented in the second haul).[4] If this requirement was not satisfied, a supplementary haul was made to augment the size of the recapture sample.

Trout of each age group in the recapture sample were processed as follows: (1) Marked and unmarked fish were enumerated, and the population estimated by multiplying the total number of fish in the recapture sample by the reciprocal of the fraction of marked fish recaptured.[5] (2) All (or a maximum of 60) trout were measured to the nearest 0.1 inch and weighed to the nearest 0.01 pound. Fork lengths were recorded in 1952, both fork and total lengths in 1953–55, and total lengths only from 1956 on. Mean fork lengths (from inventory

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[4] Provided that the usual assumptions concerning validity of Petersen estimates had been met.

[5] Ricker (1958, p. 84) points out that although Bailey's modification of this formula provides a less biased estimate, there is little difference between the two when large numbers of marked individuals are recaptured, as was the case here.

data of 1952 and early 1953) were transposed to total lengths before being entered on cards, utilizing the following total length (Y) – fork length (X) regressions (inches) computed from data obtained in 1953–55, when both measurements were taken at pond inventories:

Brook trout:
$\hat{Y} = 1.0389X + 0.05 \ (n = 194)$

Rainbow trout:
$\hat{Y} = 1.0593X - 0.03 \ (n = 138)$

Brook × brown hybrid:
$\hat{Y} = 1.0625X - 0.01 \ (n = 74)$

Brook × lake hybrid:
$\hat{Y} = 1.0511X + 0.11 \ (n = 36)$

Lake × brook hybrid:
$\hat{Y} = 1.0726X - 0.07 \ (n = 38)$

Scale samples were seldom taken because the age group(s) of trout present in each pond were known, and readily distinguishable on the basis of size.

Reliability of Population Estimates

Comparison of Estimated and Known Numbers

To assess the accuracy of Petersen estimates of trout populations in farm ponds, inventories were conducted in 15 ponds that had been stocked 11 to 26 days earlier with known numbers of brook or rainbow trout — 5- to 8-inch fall fingerlings in most cases. Pond acreages ranged from 0.1 to 1.8, with a mean of 0.5. Only 2 hauls with a 150-foot bag seine were made for each population estimate.

Means and ranges of percentage deviations between numbers stocked and estimated populations are given in table 4. These data indicate that the 2 criteria of sample adequacy employed jointly in the field provided population estimates whose maximum error seldom exceeded 10 percent. There was no evidence of bias in the estimates where both sampling criteria were satisfied (algebraic mean –1.1, table 4), which suggests that the means of mortality rates determined from these population estimates were likewise unbiased.

Relative vulnerability of marked and unmarked fish to capture in second seine hauls was no different (and population estimates were no less accurate) in 10 of the ponds where 15 to 20 minutes elapsed between first and second seine hauls than in the 5 ponds where this interval was 1 to 18 days.

Agreement Between Successive Population Estimates

Twenty-five ponds were inventoried twice in the same season — some to determine agreement between 2 successive population estimates, some because first estimates were judged unreliable by one or both of the sampling criteria described in the preceding section. Intervals between first and second estimates ranged from 30 minutes to 59 days, with a mean of 15 days, and 21 (84%) of the intervals were less than 30 days.

Discrepancies between 2 successive population estimates were less than 5 percent of the mean in 13 ponds, between 5 and 10 percent in 3 ponds, and between 20 and 93

Table 4. **Accuracy of Petersen estimates of trout populations in 15 farm ponds stocked 2 to 5 weeks before inventory**

(Data categorized by criteria used in field to distinguish adequate from inadequate samples)

Marked fish taken in recapture haul comprised:	No. of ponds	Deviation of estimated population from no. stocked, expressed as percent of latter: Mean, Absolute	Mean, Algebraic	Range
1/3 or more of no. marked and released; *also* 1/3 or more of total fish in recapture haul	9	5.6	−1.1	−11 to +10
Less than 1/3 of no. marked and released, *or* Less than 1/3 of total fish in recapture haul*	6	10.6	−9.2	−21 to +3

* In practice, such samples were considered inadequate, and additional steps were taken to obtain more reliable estimates. See *Procedures*.

percent in the remaining 9 ponds. In 6 of these last, the sampling criteria had not been met in one or both estimates of each pair of estimates; in the other 3 ponds sampling criteria had been met, discrepancies between successive estimates ranged from 20 to 23 percent, but in 2 of these comparisons the numerical discrepancies were only 6 fish each.

Sample Sizes

Percentages of estimated trout populations captured in individual seine hauls are summarized in table 5. This tabulation includes data from samples that were considered inadequate for reliable population estimates. In a pair of seine hauls that just meet both of the above-mentioned criteria for a reliable estimate (which in effect require that to be acceptable each haul must have captured one-third of the total population), the total fraction of the population captured in 2 seine hauls (not counting recaptures) is

$$.33 + (.33 \times .67) = .55$$

In this study, therefore, a minimum of 55 percent and an average of more than 80 percent of the reliably estimated populations were actually counted in the 2 hauls with a 150-foot seine. Comparable figures for inventories made with a 75-foot seine are 55 to 65 percent, respectively. With both the 75- and 150-foot seine, the mean proportions of total populations captured in first and in second seine hauls were approximately equal; however such close agreement was not characteristic of individual population inventories.

Table 5 does not include data

Table 5. **Indices of sample sizes in 221 Petersen estimates of trout populations in farm ponds**

(each estimate based on 2 hauls of a bag seine of the specified length)

Bag seine length (ft)	Number of pop. ests.	Statistic	Percent of estimated population captured in: First haul	Percent of estimated population captured in: Both hauls*	Percent of marked fish recaptured in second haul†
150	206	Mean	58‡	79	56
		Range	8–100	18–100	5–100
75	15	Mean	45	63	42
		Range	4–94	9–100	5–88

* Number of fish captured in first haul (marked and released) plus number of unmarked fish captured in second haul, as percentage of estimated population.

† Identity with percentage of estimated population captured by second haul, in Petersen formula.

‡ Saila (1952) reports an average of 51 percent for trout population estimates in 70 farm ponds.

from 36 inventories (made with a 150-foot seine) of ponds with estimated populations of 8 fish or less, because data from such inventories are erratic, and percentages are not comparable with those tabulated. Such ponds were frequently seined 3 or more times to obtain population estimates that were considered reliable. In these pond inventories, the total number of (different) fish captured averaged 96 percent of the estimated population, and the range was 67 to 100 percent.

Terminology and Notation

Because ponds were stocked and inventoried in spring and/or fall, references to trout ages are by half years. Actual ages (from an average January 1 hatching date) are 3 months older than the conventional half-year age designations indicate. Thus age I trout would be approximately 15 months old when inventoried in April or May. When inventoried the following fall (October–November), they would be designated age I+ (actually about 21 months old). The term *age interval* denotes the period of life between 2 successive ages (and between 2 corresponding pond inventories). The half-year age interval indicated in the above example would be designated I–I+. *Inventory year* denotes the calendar year in which the *end* of a particular age interval was reached.

Trout stocked in the spring at age 0 (3 months old) are referred to as *spring fingerlings* (abbreviated SF); those stocked in the fall at age 0+ (9 months) are designated *fall fingerlings* (FF). A planting in a pond where no holdovers from earlier plantings exist is termed a *new stocking*, to distinguish it from a *restocking*, or planting made where holdovers still remain.

For data analysis, the experimental ponds were classified in 2 categories of water supply:

Spring-fed (S) — a pond supplied by permanent springs extensive enough to maintain some outflow from the pond at virtually all times.

Runoff (R) — a pond apparently supplied entirely by runoff water from the surrounding watershed, as indicated by no outflow during summer months (June through September), except after occasional heavy rains. Water levels in such ponds typically dropped 12 to 18 inches during dry periods.

Abbreviations used in tables and figures for various salmonid species are as follows:

Bk......Brook trout
LT.....Lake trout
Bn......Brown trout
Rb.....Rainbow trout

In designating hybrids, the male parent species is given first. Thus Bk × Bn indicates progeny of male brook trout and female brown trout.

Symbols and terms used to denote fish population statistics are those given and defined by Ricker (1958), with only minor exceptions in the terminology of certain growth and mortality rates, as noted parenthetically in the following list of symbols commonly employed in this paper:

a.......Total mortality rate
m.......Conditional (= "annual") fishing mortality rate
n.......Conditional (= "annual") natural mortality rate
i........Coefficient (= instantaneous rate) of total mortality
p.......Coefficient (= instantaneous rate) of fishing mortality
q.......Coefficient (= instantaneous rate) of natural mortality
u.......Rate of exploitation; expectation of fishing death
v........Expectation of natural death
l........Total length, inches, of individual fish
w.......Weight, pounds, of individual fish
g.......Coefficient (= instantaneous rate) of growth
N......Number of fish in a population, per surface acre
W......Weight of fish in a population, per surface acre
C.......Catch, in numbers
Y.......Catch, by weight

Unless otherwise noted, the terms *natural mortality rate* and *fishing mortality rate* will mean the conditional rates n and m, respectively.

Symbols and definitions used in general statistics follow Snedecor (1956).[6] A circumflex ($\wedge$) denotes an estimated value; a bar over a symbol ($\bar{\ }$) represents a mean. The subscript ($_o$) denotes the start of some period of time, and the subscript ($_t$) the end of a period or some other designated time. Delta (Δ) indicates a finite change. For example, the phrase "increment in

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[6] Note that n designates the number of observations in a sample, whereas *n* indicates natural mortality rate.

mean fish weight equals mean fish weight at the end of the period minus mean fish weight at the start of the period" would be expressed symbolically:

$$\Delta\overline{w} = \overline{w}_t - \overline{w}_o$$

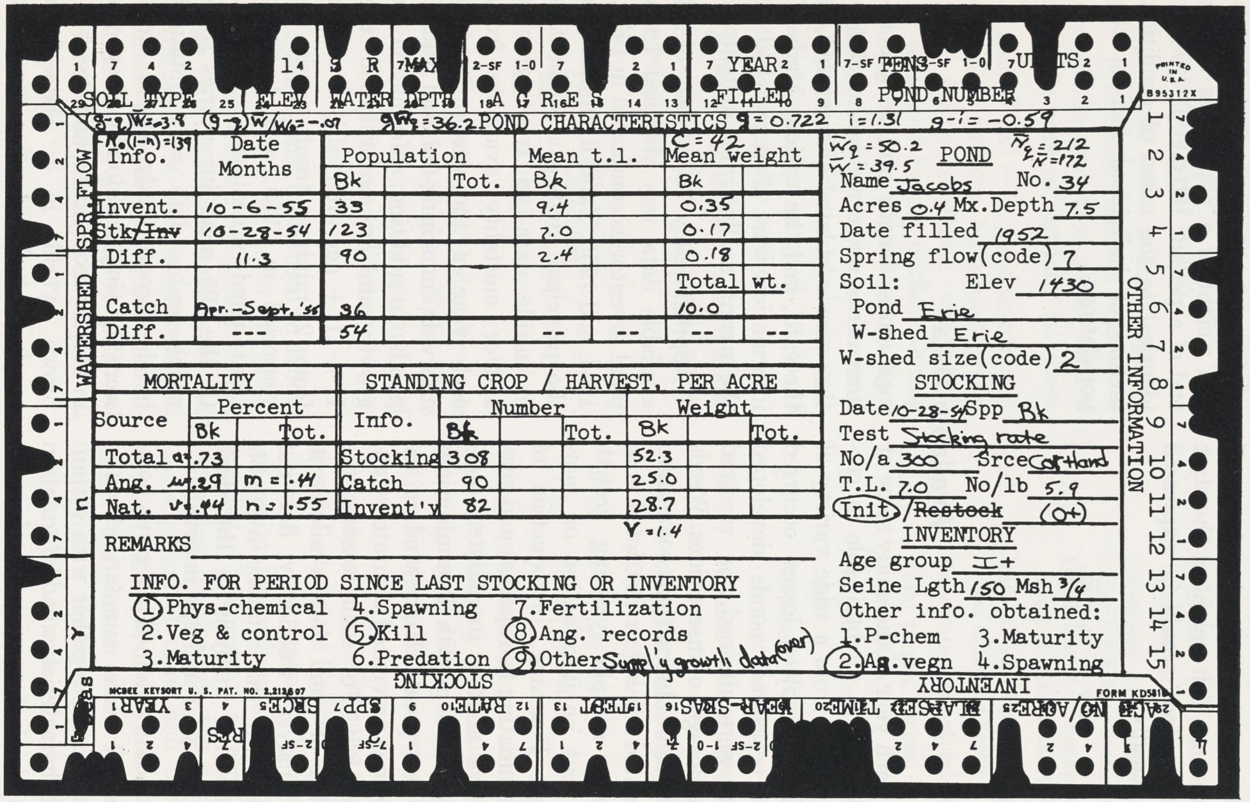
A "condition factor" as used here, was computed from the mean length and weight of a population at the end of a period: 100,000 w_t/l_t^3. Not identical to the mean of condition factors of individual fish in the population.

Available Data

In each year of the study some or all data were unobtainable in certain ponds, from a wide variety of causes. Complete losses occurred when occasional ponds developed leaks, were drained, or received lethal dosages of insecticides. Weeds and bottom obstructions sometimes prevented seining or restricted it to a single sample (yielding growth data but no information on mortality). Poaching, introduction of contaminating fish species, and size-selective angling invalidated mortality and/or growth determinations in a few ponds. High wind or ice sometimes prevented accurate weighing of fish. For such reasons, the number of pond data available in one analysis frequently did not agree with the number available for another analysis in the same calendar year and age interval.

The data obtained in a given pond inventory were summarized on a keysort card, together with certain pond characteristics and information from the last previous stocking or inventory of that population ½ or 1 year earlier. Mortality rates, standings crops, length and weight increments, and certain other statistics were calculated and entered on the card, and the various kinds of information were then punched in the margin, as illustrated in figure 1.

Approximately 70 percent of all available data was obtained from pond inventories conducted in 1953, 1954, and 1955. Table 6 summarizes the principal kinds and quantities of usable data on trout growth and/or mortality available from each year of the study, by age intervals, in spring-fed and runoff ponds. In addition, information on growth and/or mortality in the II+-III+ age interval is available from 2 rainbow trout ponds inventoried in 1955, and 1 brook trout pond inventoried in 1958. Of the 195 pond inventories from which usable data were obtained in the 7-year study, brook trout were the single or dominant species in 141, rainbows in 46, and brook × brown hybrids in 8. Data from ponds stocked with other species or hybrids were too fragmentary to provide much useful information.



$(g-i)\bar{W} = -3.8$ $(g-i)\bar{W}/W_0 = -.07$ $g\bar{W}_g = 36.2$ POND CHARACTERISTICS $g = 0.722$ $i = 1.31$ $g-i = -0.59$

$N_0(1-n) = 139$ $C = 42$

Info.	Date Months	Population			Mean t.l.		Mean weight	
		Bk		Tot.	Bk		Bk	
Invent.	10-6-55	33			9.4		0.35	
Stk/~~Inv~~	10-28-54	123			7.0		0.17	
Diff.	11.3	90		—	2.4		0.18	
							Total wt.	
Catch	Apr.-Sept. '55	36					10.0	
Diff.	---	54			--	--	--	--

MORTALITY

Source	Percent		
	Bk		Tot.
Total	a = .73		
Ang.	u = .29	m =	.44
Nat.	v = .44	n =	.55

STANDING CROP / HARVEST, PER ACRE

Info.	Number			Weight		
	Bk		Tot.	Bk		Tot.
Stocking	308			52.3		
Catch	90			25.0		
Invent'y	82			28.7		

$Y = 1.4$

REMARKS

INFO. FOR PERIOD SINCE LAST STOCKING OR INVENTORY

[✓ 1.Phys-chemical] 4.Spawning 7.Fertilization
2.Veg & control [✓ 5.Kill] [✓ 8.Ang. records]
3.Maturity 6.Predation [✓ 9.Other] Supp'l'y growth data (over)

$\bar{W}_g = 50.2$ $\bar{W} = 39.5$ POND $\bar{N}_g = 212$ $\bar{N} = 172$

Name Jacobs No. 34
Acres 0.4 Mx.Depth 7.5
Date filled 1952
Spring flow(code) 7
Soil: Elev 1430
Pond Erie
W-shed Erie
W-shed size(code) 2

STOCKING

Date 10-28-54 Spp Bk
Test Stocking rate
No/a 300 Srce Cortland
T.L. 7.0 No/lb 5.9
[✓ Init.] /~~Restock~~ (0+)

INVENTORY

Age group I+
Seine Lgth 150 Msh 3/4
Other info. obtained:
1.P-chem 3.Maturity
[✓ 2.Ag.vegn] 4.Spawning

Figure 1. Keysort card used for tabulating data obtained in two successive inventories of a farm pond trout population and the intervening half year or year.

Table 6. **Numbers of spring-fed and runoff ponds in which usable data on trout mortality and/or growth were obtained in the years 1952 through 1958**

Inventory year	Species*	Fish age interval and pond water supply category†																						
		Half-year data										Whole-year data								Age combinations‡		Totals		
		0–0+		0+–I		I–I+		I+–II		II–II+		0–I		0+–I+		I–II		I+–II+						
		R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	All ponds
1952	Bk	12	3																	1		13	3	16
	Rb																			1		1	0	1
1953	Bk	4	1	3	3	3							1	7	3					1	1	18	9	27
	Rb			1		2						1		5	2			1			1	10	3	13
	Bk Bn		1																			0	1	1
	Comb.		1																		3	0	4	4
1954	Bk	4	4	2		2								5	1		1		4	3	1	16	11	27
	Rb																	2		1	1	3	1	4
	Bk Bn				1		1															0	2	2
	Comb.					1	1						1		1						6	1	9	10
1955	Bk			1	1	1							1	2	6			3	1	3	3	10	12	22
	Rb													1	1					1	1	2	2	4
	Bk Bn	1							1													1	1	2
	Comb.			1										1						4	5	6	5	11
1956	Bk				1																2	0	3	3
	Rb			4	4		1		1		1				1							4	8	12
	Bk Bn								1													0	1	1
	Comb.							1													3	1	3	4
1957	Bk	1	4																		1	1	5	6
	Rb				1						1											0	2	2
	Comb.		1		1	1															6	1	8	9
1958	Bk			1	2																	1	2	3
	Comb.							1														1	0	1
Totals	Bk	21	12	7	7	6							2	14	10		1	3	5	8	8	59	45	104
	Rb			5	5	2	1		1		2	1		6	4			3		3	3	20	16	36
	Bk Bn	1	1		1		1		2													1	5	6
	Comb.		2	1	1	2	1	2					1	1	1					4	23	10	29	39
	All ponds	22	15	13	14	10	3	2	3		2	1	3	21	15		1	6	5	15	34	90	95	185

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* See text for species abbreviations. Comb. = ponds containing more than 1 species.

† R = runoff water supply; S = spring water supply (explanations in text).

‡ Ponds containing more than 1 age group of fish, including those with fish older than age II+.

The following 2 sections are concerned with results from 2 specialized and rather limited areas of investigation (hybrids and special strains; reproduction and artificial spawning areas). The remainder of the paper is concerned with analyses of the main body of data on trout growth and mortality in New York farm ponds, determinations of average standing crop, and implications of the findings to management and future research.

Hybrid and Wild Trout

Hybrids

Survival and growth

In November 1952, various crosses were attempted between brook, brown, rainbow, and lake trout with the primary object of comparing the survival of such hybrids to that of brook and rainbow trout in farm ponds.

Data on survival to the free-swimming fry stage are listed in table 7, with comparable data obtained at the Benner Spring Research Station by Buss (1956). There is a general similarity of trends in the 2 sets of data. Buss (*op. cit.*) indicates that transportation difficulties may have adversely affected the survival of his brook × lake and lake × brook trout crosses. Stenton (1952) reported a survival of 75 percent with the brook × lake trout cross. Some of the difference in success of the brook × brown and brown × brook trout hybrids at the 2 stations might have been attributable to the fact that most of the parents used for this cross at Cornell were taken from natural waters, whereas Buss employed hatchery stock.

Table 7. **Survival of salmonid hybrids to free-swimming fry stage, as percentage of number of eggs incubated**

(Data on crosses made at Cornell Fishery Laboratory [1952] and at Benner Spring Research Station [Buss, 1956])

Hybrid*	Survival (percent)	
	Cornell	Benner Spring†
Bk × LT....	78.7	28.0
LT × Bk....	75.6	0.7
Bk × Bn....	16.8	5.0, 4.0
Bn × Bk....	15.6	0.5
Rb × Bn....	0	0.0, 0.0
Bk × Rb....	0	0.0, 0.6

* Paternal species listed first.

† Two numbers in same row indicate 2 years' data.

Brook × lake trout hybrids in 2 ponds and lake × brook trout hybrids in 1 pond survived to age I+ and reached mean total lengths of 11.7, 12.0, and 12.0 inches, respectively. A number of confounding factors make it impossible to draw firm conclusions about the survival potential of these hybrids, but some of the data suggested that they may have been less well suited for a farm pond environment than other salmonids tested because of lower temperature tolerance. Growth and survival of brook × brown trout hybrids did not differ measurably from those of brook and rainbow trout, and are therefore included in the major sections on trout growth and mortality to follow.

Maturity

Three ponds containing age I+ brook × brown trout hybrids and 1 pond with age I+ brook × lake trout hybrids were inventoried in mid-November 1954. In each pond, all fish taken were tested for ripeness, and samples of both sexes were dissected and the reproductive tracts examined. None of the brook × brown trout hybrids were ripe (in contrast to the majority of brook trout of this age in New York farm ponds), and dissection showed very retarded and imperfect development of both male and female gonads. None of the female brook × lake trout hybrids were ripe; on dissection the ovaries appeared normal but juvenile. Small amounts of milt could be expressed from about 10 percent of the males of this cross, and the testes of dissected specimens appeared normal and well-developed. Secondary sex characteristics of body form and coloration were prominent in the males and females of both hybrids.

Conclusions

In farm ponds, brook × brown trout hybrids exhibited growth and survival that were comparable with those of brook trout and rainbow trout. They were popular with anglers because they took a lure readily[7] and fought hard. However, the low survival of this hybrid to the fry stage would make it impractical to propagate for farm pond stocking on a large scale.

Brook × lake trout hybrids may or may not be thermally adapted for existence in New York farm ponds. At best, however, their growth and survival in this environment are not measurably superior to those of brook or rainbow trout. It seems unlikely that propagating this hybrid for stocking in farm ponds such as those described here would offer enough advantages over domestic brook or rainbow trout to compensate for the greater difficulty of securing lake trout brood stock.

Wild Trout

Equal numbers of a domestic (Cortland) and of a wild (Cranberry Lake) strain of brook trout were stocked in each of 4 ponds in October 1952, at age 0+ (table 3). Data on growth and mortality of each group are available for the first, second, and third years of life from one pond, and for the first and the second plus third years (combined) from another pond. Natural mortality rates of the 2 strains were virtually identical in both ponds. If one of the above strains was genetically superior to the other with respect to survival potential, the environments provided by these 2 farm ponds were not adverse enough to reveal such differences.

Increments in mean total length of each strain from age 0+ to age II+ were the same in one pond, 1 inch greater for the domestic strain in the other pond.

When the above ponds were inventoried in November of 1953 and 1954 (fish ages I+ and II+,

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[7] See section on angling mortality.

respectively), all trout captured were tested for ripeness. In both years in both ponds, all males of both strains were ripe, and most females of both strains were either ripe or spent.

Reproduction, Artificial Spawning Areas, and Egg Incubators

Maturity and Reproduction

Information on the age and season at which brook and rainbow trout reached maturity is limited to observations on ripeness[8] of brook trout (ages 0+ to II+) in 16 ponds and of rainbow trout (ages I to III+) in 8 ponds. No ripe brook trout of either sex were observed in any period other than November–December. Many (but not all) brook trout males were usually ripe at age 0+; all were ripe at age I+. All I+ females tested in 4 ponds, and all II+ females tested in 4 ponds, were ripe. Data for rainbow trout are less informative. Ripe rainbow males were observed in November in 3 ponds (ages II+ to III+), and in April in 3 ponds (1 pond each of age I, age II, and age III fish). Age III females tested in 2 ponds in April were ripe; none of the females (age III+) tested in 3 ponds in November were ripe. Saila (1952) tested 4 age II female rainbow trout from a farm pond and found them to be ripe.

Brook trout successfully reproduced at least twice in each of 2 ponds. Both of the ponds were fed by exceptionally large springs. In 1 of these ponds where spring inflow was through the pond bottom, a maximum of 33 age I+ fish spawned in the fall of 1955. An estimated population of 24 5.6-inch young (age 0+) were present a year later, in the fall of 1956, at which time the 6 surviving parents (now II+) spawned again. In the fall of 1957 the total estimated population of young from these 2 successive spawnings was 88 fish, from 5.3 to 8.3 inches long (ages 0+ and I+). The second pond had a spring inlet with a flow of about 1 gallon per minute. In the fall of 1953 a population of 35 age I+ brook trout spawned successfully along the gravelly shoreline adjacent to the screened-off inlet. An estimated population of 22 age II, 9-inch progeny remained in the spring of 1956. Brook trout again reproduced in this pond in the fall of 1956, but quantitative results were not obtained. In a third pond, having a permanent but small spring in the bottom, evidence of reproduction was obtained only once in the course of 7 years, when an estimated 5 0+ brook trout were produced by spawning of an estimated 6 I+ fish the previous fall.

With the above exceptions, no other indication of successful reproduction was obtained in this 7-year study involving 70 farm ponds, although fall spawning activities

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[8] That condition in which eggs or sperm can be manually expressed by the usual hatchery technique.

(including egg deposition) by brook trout were often observed in the shallower areas of ponds where there was some gravel in the predominantly clay bottom. Most farm ponds of this area do not provide the combination of substrate and water supply characteristics necessary for reproductive success of brook trout, much less rainbow trout. The available data suggest that mortality of naturally produced trout in these ponds is usually high, probably due in large part to predation by older age groups, coupled with lack of cover for the young.

The remainder of this section concerns descriptions and tests of devices to promote hatching of trout eggs in farm ponds. Many readers may wish to skip directly to the following section on growth.

Artificial Spawning Areas

Saila (1952) filled a wooden trough (8 × 28 × 72 in.) with gravel and placed it in the spring inlet to a pond so that the trough was readily accessible from the pond and some of the spring water flowed through the gravel. He created gravel areas 8 inches deep and about 6 feet in diameter near the shores of 2 other ponds, 1 at the entrance of a spring feeder. In 1953 the author constructed areas similar to these last in 2 other ponds, and made observations on all 5 areas in November of 1952, 53, and 54. The brook trout in these ponds sometimes utilized some of these areas for nest-digging and/or egg deposition, but the redds quickly became silt-covered after being deserted by the fish, and there was no evidence that any of these artificial spawning areas ever produced a hatch.

Egg Incubators

Various devices for incubating trout eggs in farm ponds were tested from 1952 through 1955. After fertilization and water-hardening, "green" brown trout eggs were placed in a Vibert plastic hatching box and planted in gravel in a very small spring feeder to one pond, in the manner recommended by the inventor (Vibert, 1949). Other green eggs were incubated in a device consisting of a screen tray suspended above a gravel box and protected from silting by a plywood roof. Two of these devices were placed in each of 2 ponds. All of the above experiments resulted in total egg mortality — apparently caused by silting and suffocation of the eggs.

Eyed brown trout eggs in Vibert boxes were suspended over gravel in 5 open-ended cans that were placed in various locations around one pond. All of these eggs died before hatching except for a 50 percent hatch in one box that was located near the pond's intake box.

Another device that was tried consisted of a rectangular electrical junction box, 3 × 4 × 12 inches, in which was suspended a tray or a Vibert box containing 500 to 700 eggs. The box was sealed except for a 1-inch hole in the bottom (below the eggs) and a ¼-inch nipple in the top of the box connecting to an 8-foot length of rubber tubing. The box was suspended in a cage of window screening, 8 × 12 × 16 inches high, which in turn was suspended from the top of the pond's trickle tube (standpipe) so that the incubating box was about 3 feet below the water surface. The rubber hose was led up over the top of the trickle tube, and down inside it for about 5 feet, after starting the hose siphoning. In all but 1 trial of these devices, water continued to siphon up through the hole in the bottom of the box and through the eggs throughout the winter, despite sub-zero temperatures and a 12-inch ice cover. As the eggs hatched, fry could exit through the hole in the bottom of the box into the screen cage, and presumably could escape over the top of the cage and into the pond when they became free-swimming.

In the winters of 1953–54 and 1954–55 tests of these siphon incubators were conducted in Cornell Fishery Laboratory ponds, and in each case control lots were incubated simultaneously by conventional hatchery methods in the Laboratory, which had the same water supply and water temperatures as the ponds. In 1954, all of the green eggs of brown trout incubated from January to April in 6 boxes (1 box containing a tray and 1 a Vibert box in each of 3 ponds) died before hatching. A single box stocked in March with eyed eggs of the same lot produced a hatch, but a flaw in the screen cage enclosing this box made it impossible to evaluate the success of this experiment quantitatively.

In 1955 eyed brook trout eggs were incubated from January to March in 4 boxes — 1 of each type in each of 2 ponds — and 2 control groups of the same egg lot were incubated in the laboratory. Water temperatures ranged from 34° to 37° F during the experiment. In 1 incubator (tray type) in which the siphon was inoperative for 12 days, the hatch was only 10 percent; in the other 3 incubators hatches were 34, 55, and 57 percent. Hatches in the 2 control lots were 47 and 49 percent. Unfortunately the brook trout eggs available for these 1955 tests appeared to be of poor quality from the start; many of them were white-spotted.

Green rainbow trout eggs from wild brood stock were incubated in 2 siphon boxes (1 of each type) in 1 pond, while 4 control lots of 200 eggs each were incubated in hatchery troughs. All eggs were immersed for 1 minute in a 1:30,000 solution of malachite green immediately preceding the experiment. Water temperatures ranged from 44° F when tests were started on April 2, to 63° F on April 15 when hatching was completed in the control lots and the experiment was terminated. About 76 percent of the eggs in each control lot hatched, but all eggs in both siphon incubators were dead and were heavily coated with silt.

The experiments described above were rigorous tests of the siphon incubators because the ponds in which they were conducted are fed continually by water from a stream that often carries a heavy silt load. In one of several tests of eyed brook trout eggs in Maine farm ponds (Anonymous, 1951), 600 eggs suspended on screening above a tray of gravel in the bottom of a pond produced a hatch of 588 eggs, despite the apparent absence of spring inflow at the site.

Growth

Growth data were analyzed to determine:

- The effects of season and calendar year, pond water supply (spring vs. runoff), fish species and age, initial size of fish, and population density (number of fish per acre) on growth rate. Other variables examined — some less critically because of limitations in the available data — were elapsed time between size determinations, fertilization and pond chemistry, soil type, and the age, size, and elevation of ponds.
- Mean growth increments in each age interval. These data were particularly needed, in conjunction with comparable mean natural mortality rates, for computing average standing crops and potential yields in trout pond populations at various ages.
- Relative utility of 3 growth indices.

The mean length ($\bar{l}$) or weight ($\bar{w}$) of the fish population of a particular pond at a particular time (stocking or inventory) was the basic unit employed in growth determinations. This was necessary because it was not feasible to maintain the identities of individual fish in a given pond population from one sampling to the next. Thus the measure of length increments ($\Delta\bar{l}$) in a pond population between time "o" and time "t" was $\bar{l}_t - \bar{l}_o$. Similarly, the coefficient of growth, g, was of necessity determined from means rather than from individual fish. For a given pond population in a given time interval, as used here:

$$\bar{g} = \log_e \left(\frac{\bar{w}_t}{\bar{w}_o} \right)$$

This might be termed a *coefficient of mean growth,* to distinguish it from a mean of the growth coefficients of individual fish, with which it is not strictly comparable.

Unweighted means were used to describe the average growth in a group of ponds. For example, the average length increment in such a group would be computed by summing the individual $\Delta\bar{l}$'s and dividing by the number of ponds. The alternative procedure would be to determine a weighted mean by obtaining the mean length of the pooled samples of individual fish from all ponds at time o, repeating the process at time t, and subtracting the former from the latter. As will be seen, individual ponds were one of the largest sources of variation in growth, and for this reason, among others, a mean giving equal weight to the growth increment in each pond was far preferable to one that gave most weight to the pond in which the largest sample of fish was measured.

Rank-sum tests (Dixon and Massey, 1957, p. 290) were often used to assess the significance of differences between growth data from 2 or more series of individual ponds. Sections to follow indicate that these data ($\Delta\bar{l}$, $\Delta\bar{w}$, $\bar{g}$) were by no means normally distributed; for such comparisons the rank-sum test is not only more appropriate (involving no assumption of normality), but also considerably more powerful than procedures, such as the t test, that are designed for normally distributed variates.

These data (and also natural mortality rates) were unsuited to multiple regression analysis for a number of reasons, the most prohibitive of all being that most of the *X* variables were not quantitative ones — season, year, pond water supply, and species, to name a few.

Variables Affecting Growth

A simultaneous subdivision of the available growth data by all the principal potential variables listed at the start of this section would render these data practically useless. This is particularly so because of the high variability in growth data between ponds and within ponds, even in situations where many sources of variation are controlled. Table 8 illustrates this point with actual data from 2 ponds, each stocked with spring fingerling brook trout in 1952 and again in 1954, and in each case inventoried the following fall (age interval 0 – 0+). Conclusions that might be drawn

Table 8. **Data on 0–0+ growth and population density in 2 ponds each stocked with spring fingerling brook trout in 1952 and 1954, and inventoried in the fall after each stocking***

Item	Pond No. 3 (spring-fed)		Pond No. 14 (runoff)	
	1952	1954	1952	1954
Stocking (age 0)				
Date	5/23	5/15	5/23	5/15
No./acre (N_o)	400	800	400	400
Mean length ($\bar{l}_o$)	2.1	1.9	2.1	1.9
Mean weight ($\bar{w}_o$)	0.006	0.001	0.006	0.001
Inventory (age 0+)				
Date	10/25	10/12	11/19	10/2
No./acre (N_t)	286	340	280	300
Mean length ($\bar{l}_t$)	6.3	6.5	8.0	6.0
Mean weight ($\bar{w}_t$)	0.098	0.120	0.213	0.104
Interim (0–0+)				
Elapsed time (mos.)	5.1	4.9	5.9	4.6
Mean no./acre ($\bar{N}$)	339	537	336	347
Mean biomass ($\bar{W}$)	11.8	12.6	16.5	10.8
Length increment ($\Delta\bar{l}$)	4.2	4.6	5.9	4.1
Weight increment ($\Delta\bar{w}$)	0.092	0.119	0.207	0.103
Coeff't. mean growth ($\bar{g}$)	2.79	4.79	3.57	4.64

* In each year, stock for both ponds were from the same hatchery lot.

from one pond about variation in growth with calendar year, population density, initial size, or elapsed time are unsupported or contradicted by data from the other pond; conclusions about differences between ponds in one year's data are unsupported or contradicted by the other year's data. This disquieting example of pond variability, while extreme, shows why it was necessary to combine data from subcategories whenever possible, to obtain meaningful information about the effect of a particular variable.

A central problem in analyzing the farm pond growth (and mortality) data, then, was to identify certain of the potential variables which, at constant levels of the other variables, bore no detectable relationship to growth. Once a potential variable had been so identified, pond data for its various levels could then be combined and thus bring more information to bear in analyzing the effect of another potential variable on growth.

The immediately following analyses of the relationships of fish species, calendar year, and pond water supply to growth are made on the premise (later substantiated) that growth in a given time interval was influenced by mean population density ($\overline{N}$, as described by Ricker, 1958, p. 27), fish age, mean size at the start of the interval, and season. In analyzing growth data for a particular age interval, information from ponds in which more than 10 percent of the population present at the start of the interval consisted of older fish from an earlier stocking was considered unusable. This was done on the assumption that in such ponds growth of the dominant age group was influenced by the population of older fish, and therefore was not comparable with growth data from ponds containing fish of virtually all one age group. Because of this restriction, plus the fact that population estimates could not be made in all inventories where growth data were obtained, and *vice versa*, the total volume of valid growth data accompanied by information on mean population density is smaller than the tabulation of all available growth and/or mortality data (table 6) might indicate.

Species

Although brook trout data comprised 53 of those 78 that were usable for assessing effects of variables, certain categories of certain variables were all or largely composed of rainbow and/or brook × brown hybrid data. Therefore it was important to evaluate growth differences between these 3 kinds of trout in farm ponds to determine whether information from all 3 sources could be justifiably combined.

Length-weight relationship. Figure 2 shows linear regressions of mean weight on mean length fitted to 88, 49, and 13 means, respectively, from individual brook, rainbow, and brook × brown trout pond populations. There was a tendency (nonsignificant) for brook trout to average slightly heavier than rainbow trout of the same

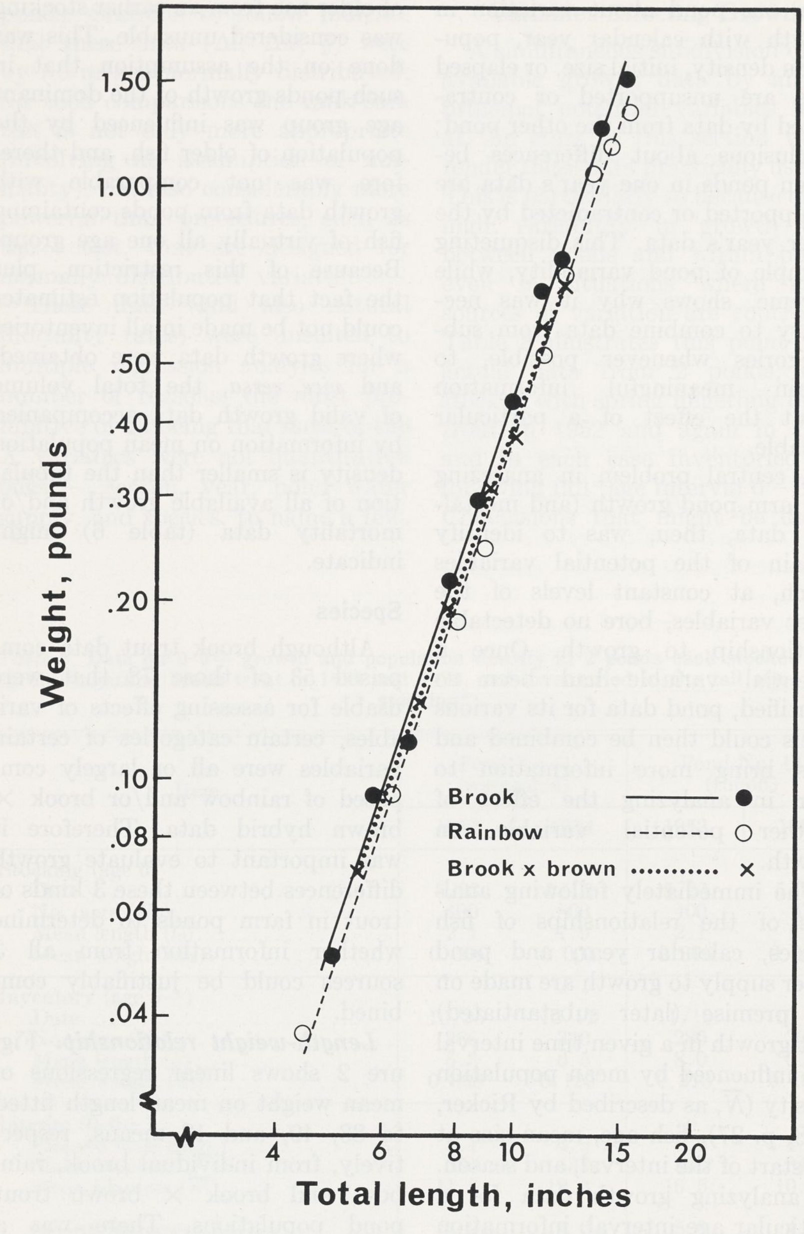

***Figure 2.* Linear regressions of weight on length for brook trout, rainbow trout, and brook × brown trout hybrids in New York farm ponds. Points are means for 1-inch length classes. Logarithmic plot.**

length. Slopes of the 3 lines do not differ significantly.

Lengths at successive ages. Unweighted mean lengths of each of the 3 kinds of trout at each half year of life were determined by simply averaging all applicable means of individual pond populations that were available in the entire body of farm pond data. The results are shown in figure 3. These pooled data are crude in that other factors (such as size at stocking and mean population density), whose effects on growth might have been confounded with species differences, are not taken into account. Nevertheless it seems unlikely that such confounding could have been so consistently fortuitous as to produce the strong similarities in growth patterns shown in the graph, had growth rates of the 3 kinds of trout differed appreciably in these ponds.

Length increments. The best growth comparisons were those available from 7 tests in which equal numbers of 2 or more kinds of trout of closely similar age and initial size were simultaneously stocked in the same pond. The kinds of trout and age intervals involved in each test are shown below:

Kinds of trout simultaneously stocked	Age intervals for which growth data obtained
Brook & rainbow	0+ — I
Brook & brook × brown	0 — 0+ — I+ 0+ — I+
Brook & rainbow & brown[9]	0 — I 0 — 0+ — I — II 0—0+—I—I+
Rainbow & brown[9]	0+ — II+

In every test, growth differences between different kinds of trout in the same pond were statistically nonsignificant. Growth relationships between kinds of trout were not consistent from one pond to the next. The growth of a given species differed far more between ponds than did the growth of any 2 species in the same pond.

Relationships of trout growth to calendar year, pond water supply, initial size of fish, and mean population density were examined on a single-species basis and on a combined-species basis. In each case, the conclusions indicated by available data on 1 species did not differ from those indicated by data from all 3 species combined, except that the combined data revealed certain relationships more clearly. Combined growth data from brook trout, rainbow trout, and brook × brown trout hybrids are employed in the sections to follow.

Inventory year and pond water supply

Figure 4 shows the data available for assessing the effects of calendar year and pond water supply (spring vs. runoff) on growth, relative to the effects of mean population density and mean length of fish at the start of the growth period (age interval) under consideration. By definition, the 0 – 0+ age interval is a summer period, and the 0+ – I age interval a winter period. Growth data for other age intervals are not included because they do not afford comparisons between calendar years.

There is some evidence in figure 4 that growth rate tended to vary

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[9] Conducted or initiated by Saila (1952).

Figure 3. **Unweighted mean total lengths of brook trout, rainbow trout, and brook × brown trout hybrids at successive ages in farm ponds.**

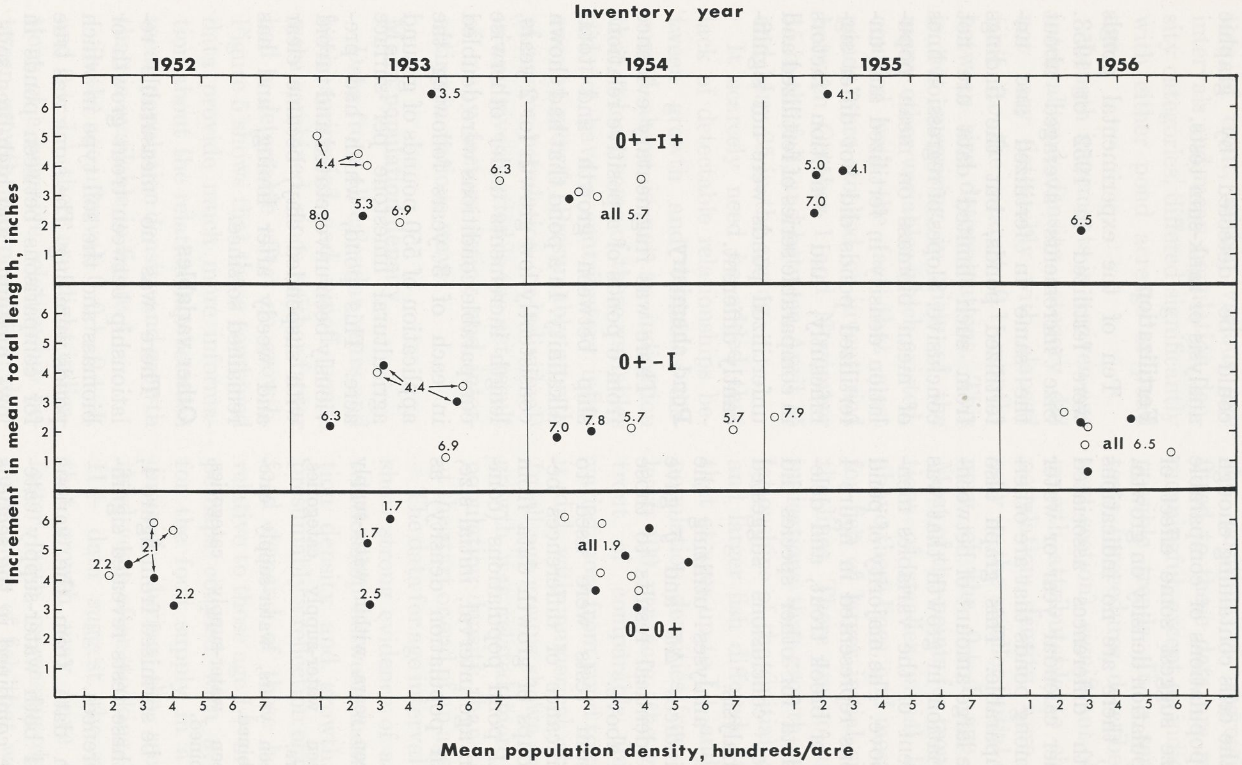

Figure 4. Relationship of increment in mean length to mean population density ($\overline{N}$) in various inventory years. Data from trout populations in 3 age intervals, in spring-fed ponds (solid circles) and runoff ponds (open circles). Number beside a point indicates mean length of that population at start of interval.

with mean initial length of fish, and some of the cells containing enough data on populations of comparable initial size suggest some effect of mean population density on growth. However, there are no indications of growth differences associated with either calendar year or water supply among ponds that are otherwise comparable. This graph also shows the large amount of between-pond variation in growth that was independent of the variables mentioned above. The majority of pond populations represented in figure 4 consisted of brook trout, and deletion of data for other species did not affect conclusions suggested by this analysis.

Graphic analyses utilizing the growth indices $\Delta\bar{w}$ and $\bar{g}$ gave virtually identical results to those described above.

Rank-sum tests were used to test significance of differences between groups of growth data from individual pond populations (comparable in age interval, initial size, and mean population density) as follows:

- Between years, within water-supply categories.
- Between water-supply categories, within years.
- Between years, water-supply categories combined.
- Between water-supply categories, years combined.

As might be surmised from figure 4, none of these tests revealed significant differences.

Growth data from the various years and both water-supply categories are combined in the sections to follow. When data thus combined were used to re-examine growth of the 3 kinds of trout, no differences could be detected by graphic analysis or rank-sum tests.

Fertilization

Ten of the experimental ponds were fertilized in 1952 or 1953. Size increments averaged about the same in fertilized and unfertilized ponds, but the findings from such limited data are not conclusive. Slopes of regression lines of mean biomass on mean population density in fertilized and unfertilized ponds did not differ significantly, and condition factors in comparable series of fertilized and unfertilized ponds were not significantly different.

Pond chemistry

There was fragmentary evidence from 6 ponds of a positive relationship between growth and total alkalinity. In a pond that had shown consistently low growth for 2 years, length increments under otherwise comparable conditions were doubled in each of 3 years following the application of 550 pounds of ground agricultural limestone per surface acre. This pond, which had previously been unvegetated and turbid with suspended clay, became clear and weedy after liming, and has remained so since.

Other variables

There was no measurable relationship between trout growth or biomass and the soil type in which ponds were dug. The same was true for comparisons between ponds in low-, medium-, and high-lime soils, and ponds in 3 categories of elevation.

Neither growth nor condition factors of trout, within various age intervals and mean population density categories, differed significantly with either pond acreage or pond age.

Length increments in a given age interval and density category did not vary detectably with elapsed time (to the nearest 0.1 month) between size determinations. This is .not surprising in view of the many other variables which existed, coupled with the fact that most ponds were stocked or inventoried between October 1 and November 15 in the fall, and between April 15 and May 25 in the spring.

It scarcely need be added that lack of detectable relationships between growth and variables discussed above is not an indication that at least some of these variables did not have a contributory influence on growth. Presumably growth of a given population (or individual) in any given period is the net result of many factors acting and interacting in various ways.

Mean population density

Data from all calendar years and both spring-fed and runoff ponds were combined, since neither factor had a detectable effect on growth. Figure 5 shows that these combined data provide much more information about the relationship between mean population density and growth than is available in figure 4.

In the age intervals 0–0+, 0+–I, and 0+–I+ there are slight indications of a negative relationship between growth and population density. However the great dispersion among points suggests that neither the linearity, the exact slope, nor the position of regression lines fitted to these data are reliable or meaningful, except as indications of possible trends. In a series of F tests (procedures described in the next section), significant changes in growth attributable to changes in population density were revealed only in the smaller initial size category of the 0+–I age interval. Most of the points for trout populations of smaller initial length lie above these lines, and most of those for fish of larger initial size below the lines. There are no substantial indications that growth-density relationships of the (initially) smaller and larger fish differed. It appears that at ages up to I+ and at mean population densities from 40 to at least 400 per acre, the growth of trout of comparable initial size varied more from pond to pond than it did with numerical abundance. In all age groups shown in figure 5, growth was related more to mean population density than to density at the start or end of an age interval.

The data for age interval I+–II+ show strong evidence of a negative relationship between mean population density and growth. This is presumably a reflection of the higher food demand of these larger fish, relative to those age I+ or younger, perhaps coupled with a tendency for the food supply in a pond to diminish during the second and third years after stocking. The I+–II+ data suggest the possibility that growth may have decreased faster, with increasing density, in populations of fish that were larger at the beginning of the interval than among those that were smaller.

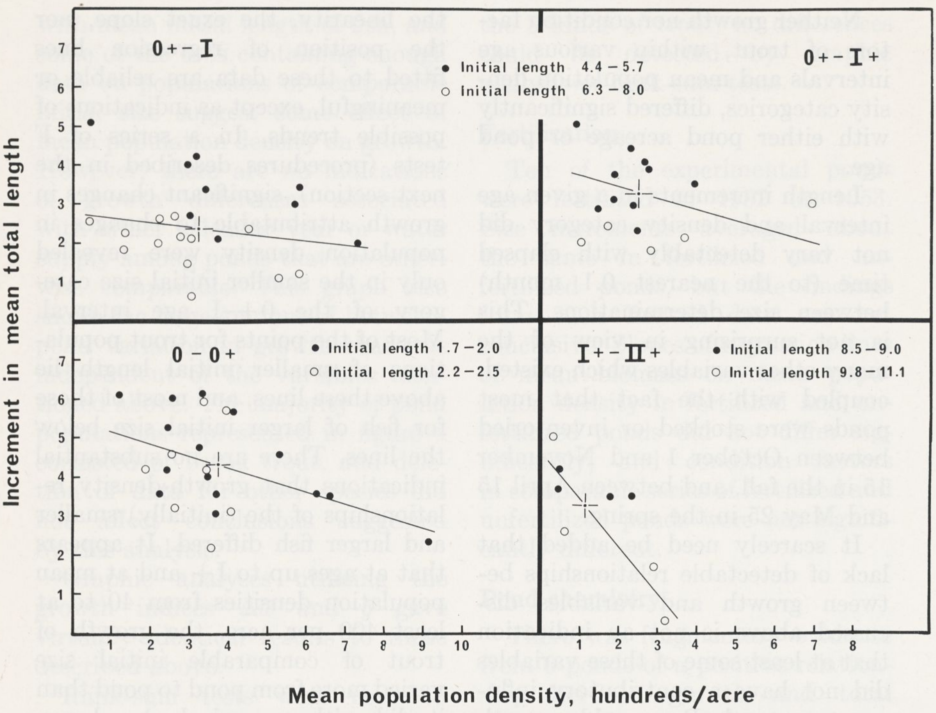

Figure 5. **Relationship of increment in mean length to mean number per acre ($\overline{N}$) for trout populations in 4 age intervals. Combined data from spring-fed and runoff ponds in all calendar years.**

Condition factors of the populations represented in figure 5 were singularly uniform, and showed little or no tendency to decline with increasing population density in any of the 4 age intervals. Analyses of the relationships of both growth coefficients and increments in mean weight to mean population densities gave results closely similar to those utilizing increments in mean length. Other relationships between these 3 growth indices are discussed in the following section.

Evaluation of Growth Indices

Sufficient data on growth, initial size, and mean population density were available from the age intervals 0–0+, 0+–I, I–I+ and 0+–I+ to permit a series of analyses to determine the extent to which each of the 3 growth indices were: (1) related to each other, (2) affected by initial size at start of a given age interval, and (3) affected by changes in population density. Combined data for the different kinds of trout, calendar years, and water supply categories were used, as in the preceding section. For analyses that involved subdividing the data into categories of mean population density, the $\overline{N}$ classes employed were

1–200, 201–400, 401–600, and 601–800 trout per acre.

Interrelationships between growth indices

Within each age interval and density class containing 5 or more data, correlation coefficients were calculated between length increment ($\Delta\bar{l}$) and weight increment ($\Delta\bar{w}$), length increment and growth coefficient ($\bar{g}$), and between weight increment and growth coefficient. Most of the correlation coefficients were between 0.780 and 0.977. In the majority of comparisons, $\Delta\bar{l}$ and $\bar{g}$ were somewhat better correlated with each other than either was with $\Delta\bar{w}$.

Size specificity

The degree to which each of the 3 growth indices is size-specific has an important bearing on their relative utility for evaluating the effects of variables on growth, because of the likelihood that effects of initial size on growth could be confounded with effects of some other variables, as, for example, calendar year (see fig. 4). In each density class (of each age interval) containing sufficient information, the growth data were subdivided according to mean size at the start of the interval. Analyses of variance[10] were made on the subdivided growth data in each density class to determine the amount of variation in growth attributable to variation in initial size. This process was repeated using each of the 3 kinds of growth data ($\Delta\bar{l}$, $\Delta\bar{w}$, $\bar{g}$), and the magnitude of the F values associated with each growth index in a given age interval and density class were compared. The 5 available comparisons of the 3 indices showed $\Delta\bar{w}$ to be consistently and markedly the least size-specific. In 3 of the comparisons, $\bar{g}$ was the most size-specific (significantly so in 2); in the other 2 comparisons, $\Delta\bar{l}$ was the most size-specific (significantly so in 1). These results seem consistent with the facts that weight increment is more constant throughout life than is length increment, and that $\bar{g}$ can be constant only during periods when increase in weight is logarithmic. Such periods in a fish's life are apparently very short (see Ricker, 1958, p. 31).

Table 9 provides an illustration of the degree to which growth trends indicated by $\bar{g}$ can diverge from

Table 9. **Initial size and growth indices for the 0–0+ age interval in 4 pond inventories (data from table 8)**

Pond	Inventory year	$\bar{l}_o$	$\bar{w}_o$	Growth indices		
				$\Delta\bar{l}$	$\Delta\bar{w}$	$\bar{g}$
14...........	1954	1.9	0.001	4.1	0.103	4.64
3...........	1952	2.1	0.006	4.2	0.092	2.79
3...........	1954	1.9	0.001	4.6	0.119	4.79
14...........	1952	2.1	0.006	5.9	0.207	3.57

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[10] One-way classification, unequal subclass numbers.

those indicated by $\Delta\bar{l}$ or $\Delta\bar{w}$. In this case much of the discrepancy in $\bar{g}$ values is associated with the differences in mean weight — proportionately large but numerically small — between the trout stocked in 1952 and those stocked in 1954.

Density dependence

Two methods were employed to assess relative utility of the 3 growth indices for evaluating the effect of mean population density on growth. The first was a series of analyses of variance paralleling those described in the preceding section, except that here the data within a given age and initial length class were subdivided into density categories, and F values were computed to estimate the amount of variation in a particular growth measurement attributable to variation in population density. Comparisons of the magnitudes of F values associated with each of the 3 indices in each of 5 available comparisons (in the 0+–I, I–I+, and 0+–I+ age intervals) suggested that changes in population density affected either $\Delta\bar{w}$ or $\bar{g}$ slightly more than they affected $\Delta\bar{l}$. However, the differences between all these F values were minor. Only 1 of them was significant ($\Delta\bar{w}$ vs. $\bar{N}$, smaller initial size category 0+–I age interval), as might be anticipated from inspection of figure 5.

Relative density dependence of the 3 growth indices was also tested by determining the coefficient of correlation between each growth index and $\bar{N}$ in each of the age–density–size categories mentioned above. Correlation coefficients were highest for $\Delta\bar{l}$ in 2 of the 5 comparisons, and highest for $\Delta\bar{w}$ in 2 others. All but 1 of the coefficients associated with 3 comparisons in ½-year age intervals ranged from 0.57 to 0.74; the 2 comparisons (from 2 size classes) in the 1-year 0+–I+ interval gave coefficients of 0.16 to 0.30. This suggests that ½-year data, as might be expected, provide more meaningful information on the relationship of growth to population density, and presumably to other factors as well. For example, the opportunities for varied interactions between the effects of temperature, food supply, and population density on growth are much greater in a 1-year than in a ½-year period.

Conclusions

The available data indicate that in several respects $\Delta\bar{w}$ is the best of the 3 growth indices for measuring the effect of variables on growth of trout up to age I+. It was less size specific than $\Delta\bar{l}$ (much less so than $\bar{g}$), appeared to be slightly more sensitive to changes in $\bar{N}$, and as well correlated with $\bar{N}$ as was $\Delta\bar{l}$. The coefficient $\bar{g}$ has great value for computing mean biomass, production, and potential yield, but its extreme size-specificity (particularly in small fish) seriously impairs its usefulness for evaluating the effects of other variables on growth, except in short time intervals and where the variable of initial size is rigidly controlled.

Results of these analyses suggest that $\Delta\bar{l}$ and $\Delta\bar{w}$ did not differ appreciably in their actual utility for measuring effects of variables, to the extent that most of the analyses were made using both indices, and in all such cases both indices yielded very similar results and identical conclusions. It is conceivable that a somewhat lower efficiency of length increment data was more than compensated for by its greater abundance (inventory conditions not infrequently prevented weighing but permitted measuring).

The fact that many more ponds were represented in the $\Delta\bar{l}$ than in the $\Delta\bar{w}$ data was an important consideration in these growth analyses, because variation between ponds was as great as, or greater than, any other source of variation. Another advantage of $\Delta\bar{l}$ (over $\Delta\bar{w}$) is its closer correlation with $\bar{g}$.

Determinations of Average Growth

Procedure and critique

All valid data[11] on increments in mean length and weight of brook trout, rainbow trout, and brook × brown hybrids, without regard to inventory year or pond water supply, and whether or not accompanied by information on population density, were summed and divided by the total number of observations to compute the mean increments for each age interval. Average values of g were computed (as before) from the average weight increments, rather than by averaging the quite erratic $\bar{g}$'s from individual ponds. Available for these determinations of average increments were 164 observations, 78 of which (shown in fig. 5) were accompanied by information on mean population density.

As noted in the preceding section, half-year growth data are much more useful than whole-year, particularly for computations of standing crop, production, and yield. Much of the supplementary growth information obtained by including data unaccompanied by population density was in half-year intervals.

Up to age I+, growth bore a slight negative relationship to population density. However, the high degree of between-pond growth variation, independent of density, clearly indicated that the reliability of mean growth data could be improved far more by substantially increasing the number of observations than by attempts to utilize weak and poorly defined growth–density relationships (see fig. 5).

Growth appeared to be much more closely related to population density beyond age I+. Apparently no serious bias was introduced into computations of average standing crop and yield of older fish when the regressions of length and weight on $\bar{N}$ were not used (in favor of increasing the amount of data for increment means by two-thirds). Using all available data, the average increments determined for the I+–II+ age interval were virtually identical with those, read from the regression lines, for the average population density in that age interval as determined from mean mortality rates.

When average length and weight increments were determined from pooled data, the demonstrated size-

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[11] Invalid data included those from ponds in which a second age group comprised more than 10 percent of the initial population of the age interval under consideration, or where some other likely source of bias existed.

specificity of the growth indices (especially $\Delta \bar{l}$ and $\bar{g}$) could have biased indications of growth relationships between age intervals if the proportion of larger to smaller fish had differed markedly in the data available from different age intervals. Fortunately the proportion was between 0.45 and 0.60 in all age intervals after addition of the supplementary growth data.

It seems reasonable to assume that the initial sizes of spring and fall fingerling trout used in these experiments approximated the range in sizes commonly available for farm pond stocking in New York.

Results

Average increments in length and weight, and growth coefficients determined from the latter, are given in table 10, with average lengths and weights at each age determined from the increments. These lengths and weights are shown graphically in figure 6. There were no reliable data for age III. Weight trends were more sensitive to seasonal influences than were length trends.[12] The overall weight trend was more linear than the length trend, as would be expected.

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[12] Seasonal growth fluctuations did not appear too large because the "seasons" being compared were approximately May 15 – October 15 vs. October 15 – May 15.

Table 10. **Lengths, weights, and growth coefficients of trout in each half year of farm pond life, computed from average increments in mean length and mean weight**

(Combined data from ponds containing brook, rainbow, or brook × brown trout hybrids, in all years. No reliable data for age III)

Age	Total length (in.)		Weight (lb)		Growth coefficient‡
	At age	Mean increment	At age	Mean increment	
0........	2.0*		0.004*		
		4.3		0.11	3.31
0+......	5.6* (6.3)†		.07* (.11)†		
		2.5		.16	1.19
I.........	8.1		.23		
		2.0		.27	0.78
I+.......	10.1		.50		
		1.3		.15	0.26
II........	11.4		.65		
		1.4		.24	0.31
II+......	12.8		.89		
		1.4		.46	0.42
III+.....	14.2		1.35		

* Average size stocked.

† Average size of trout stocked as spring fingerlings. Beyond this age most available growth data were from fall fingerling plantings, due to high mortality in the 0–0+ interval.

‡ $\text{Log}_e \left(\frac{\bar{w}_t}{\bar{w}_o} \right)$, using mean weights in fourth column. Growth coefficient for 0–0+ computed on assumption of a mean weight of 0.11 at 0+.

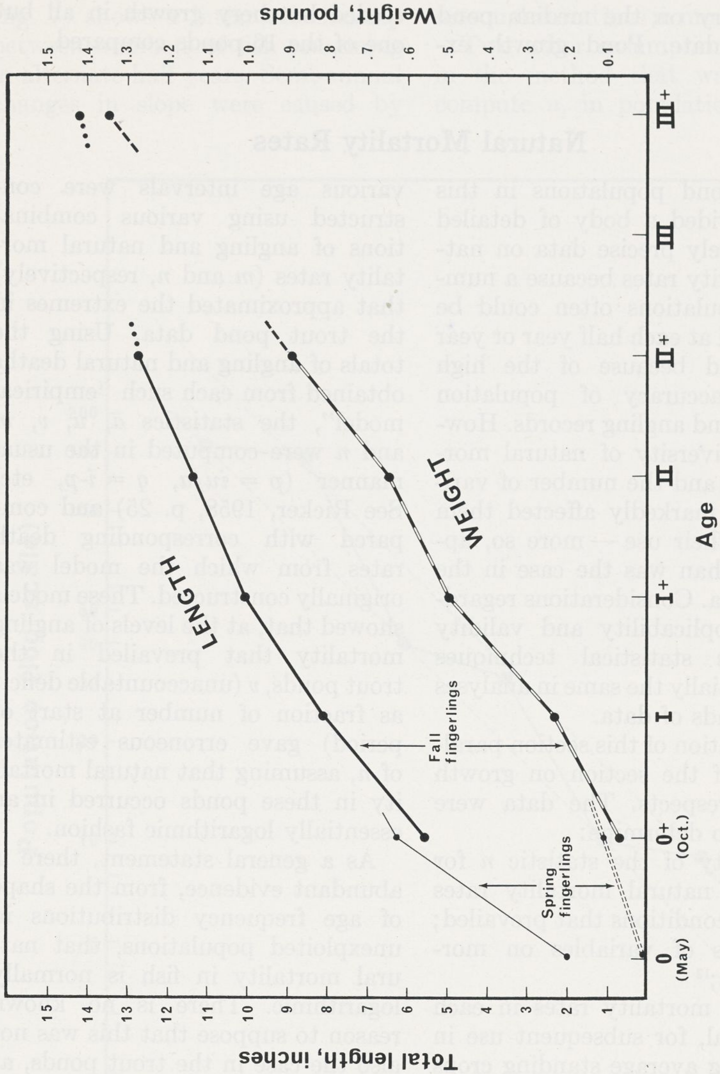

Figure 6. **Average lengths and weights of trout at each half year of life in New York farm ponds. Data of table 10.**

In the 0–0+ age interval, average growth of spring fingerlings was more rapid in ponds than in the hatchery, as shown by the short lines on figure 6. In 6 ponds stocked with spring fingerling brook trout in 1952 (Cortland Hatchery) and 10 in 1954 (Elbridge Hatchery), mean pond lengths the following fall averaged 2.4 and 1.1 inches greater, respectively, than the mean lengths of the same lots present in the hatchery on the median pond inventory date. Pond growth exceeded hatchery growth in all but one of the 16 ponds compared.

Natural Mortality Rates

Trout pond populations in this study provided a body of detailed and relatively precise data on natural mortality rates because a number of populations often could be inventoried at each half year or year of life, and because of the high order of accuracy of population estimates and angling records. However the diversity of natural mortality data and the number of variables that markedly affected them restricted their use — more so, apparently, than was the case in the growth data. Considerations regarding the applicability and validity of various statistical techniques were essentially the same in analyses of both kinds of data.

Organization of this section parallels that of the section on growth in many respects. The data were analyzed to determine:

- Validity of the statistic *n* for estimating natural mortality rates under the conditions that prevailed;
- Effects of variables on mortality rates;[13]
- Mean mortality rates in each age interval, for subsequent use in determining average standing crops and potential yields in trout pond populations at various ages.

Validity of Procedures for Estimating *n*

Artificial schedules of deaths from angling and natural mortality in various age intervals were constructed using various combinations of angling and natural mortality rates (*m* and *n*, respectively) that approximated the extremes in the trout pond data. Using the totals of angling and natural deaths obtained from each such "empirical model", the statistics *a*, *u*, *v*, *m* and *n* were computed in the usual manner ($p = iu/a$, $q = i\text{-}p$, etc. See Ricker, 1958, p. 25) and compared with corresponding death rates from which the model was originally constructed. These models showed that, at the levels of angling mortality that prevailed in the trout ponds, *v* (unaccountable deficit as fraction of number at start of period) gave erroneous estimates of *n*, assuming that natural mortality in these ponds occurred in an essentially logarithmic fashion.

As a general statement, there is abundant evidence, from the shape of age frequency distributions in unexploited populations, that natural mortality in fish is normally logarithmic. There is no known reason to suppose that this was not also the case in the trout ponds, at least within half-year intervals. The only information available for testing this assumption was from a single rainbow trout population of a quarter-acre pond that was inventoried at half-year intervals, from age 0+ to age III, and was not fished during this time. A semi-logarithmic plot of the data

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[13] For brevity, *mortality rate* is often used in this section to denote natural mortality rate.

(fig. 7) shows a linear relationship between numbers of fish remaining in alternate half years. Semi-annual changes in slope were caused by seasonal variations in mortality rate.

Two other assumptions inherent in the method that was used to compute n, in populations subject

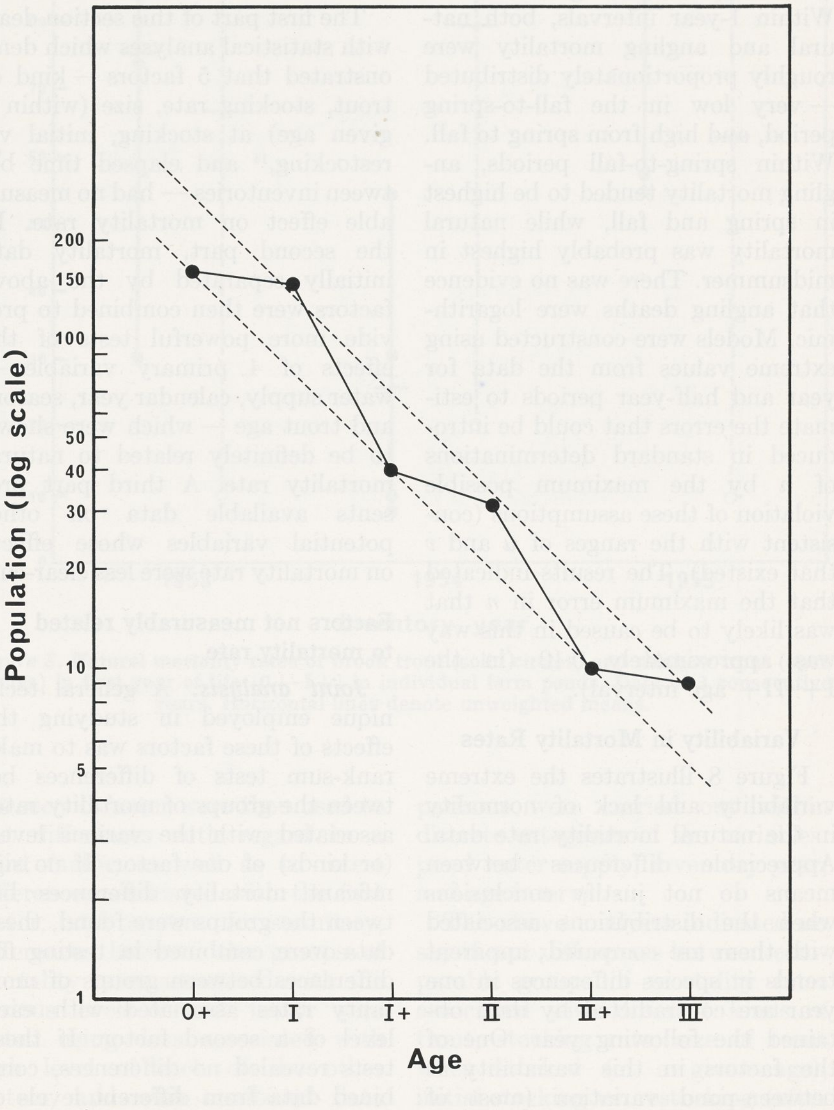

Figure 7. **Numbers of rainbow trout stocked at age 0+ and remaining in successive half-years in an unfished quarter-acre pond. Parallel broken lines fit points for alternate half-years.**

to concurrent angling mortality, are that: angling deaths are logarithmic; and incidence of deaths from natural causes and from fishing be proportionately distributed throughout the period being considered. Within 1-year intervals, both natural and angling mortality were roughly proportionately distributed — very low in the fall-to-spring period, and high from spring to fall. Within spring-to-fall periods, angling mortality tended to be highest in spring and fall, while natural mortality was probably highest in midsummer. There was no evidence that angling deaths were logarithmic. Models were constructed using extreme values from the data for year and half-year periods to estimate the errors that could be introduced in standard determinations of n by the maximum possible violation of these assumptions (consistent with the ranges of u and v that existed). The results indicated that the maximum error in n that was likely to be caused in this way was approximately 0.10 (in the I+–II+ age interval).

Variability in Mortality Rates

Figure 8 illustrates the extreme variability and lack of normality in the natural mortality rate data. Appreciable differences between means do not justify conclusions when the distributions associated with them are compared; apparent trends in species differences in one year are contradicted by data obtained the following year. One of the factors in this variability is between-pond variation (most of the data from the different years in this illustration were from different ponds). However, within-pond variability was also pronounced; figure 9 shows an example.

Effects of Factors on Mortality Rates

The first part of this section deals with statistical analyses which demonstrated that 5 factors — kind of trout, stocking rate, size (within a given age) at stocking, initial vs. restocking,[14] and elapsed time between inventories — had no measurable effect on mortality rate. In the second part, mortality data initially separated by the above factors were then combined to provide more powerful tests of the effects of 4 primary variables — water supply, calendar year, season, and trout age — which were shown to be definitely related to natural mortality rate. A third part presents available data on other potential variables whose effects on mortality rate were less clear-cut.

Factors not measurably related to mortality rate

Joint analysis. A general technique employed in studying the effects of these factors was to make rank-sum tests of differences between the groups of mortality rates associated with the various levels (or kinds) of one factor. If no significant mortality differences between the groups were found, these data were combined in testing for differences between groups of mortality rates associated with each level of a second factor. If these tests revealed no differences, combined data from different levels of

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[14] After age 0+.

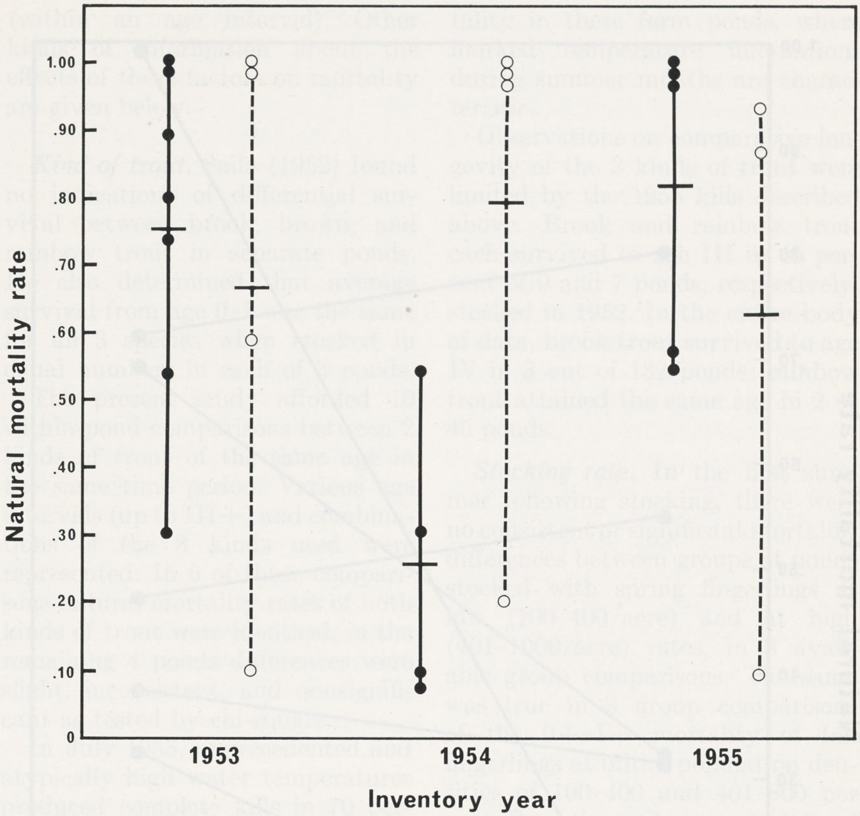

Figure 8. **Natural mortality rates of brook trout (solid circles) and rainbow trout (open circles) in first year of life (0+–I+) in individual farm ponds. Data of 3 consecutive years. Horizontal lines denote unweighted means.**

the second factor were then used to test differences with regard to a third factor, as well as to retest differences associated with the first factor, and so on. In summary, differences between the groups of mortality rates associated with the various levels of each factor were tested using data associated with each level of each of the other factors, and with combined data from all possible combinations of the other factors. All of these comparisons were carried out within discrete categories of the variables: pond water supply, inventory year, and age interval.

The above analyses indicated no significant differences between comparable groups of mortality rates associated with different kinds of trout, stocking rate, size of trout when stocked (at a given age), initial stocking vs. restocking (after the first 6 months of pond life), or elapsed time between censuses

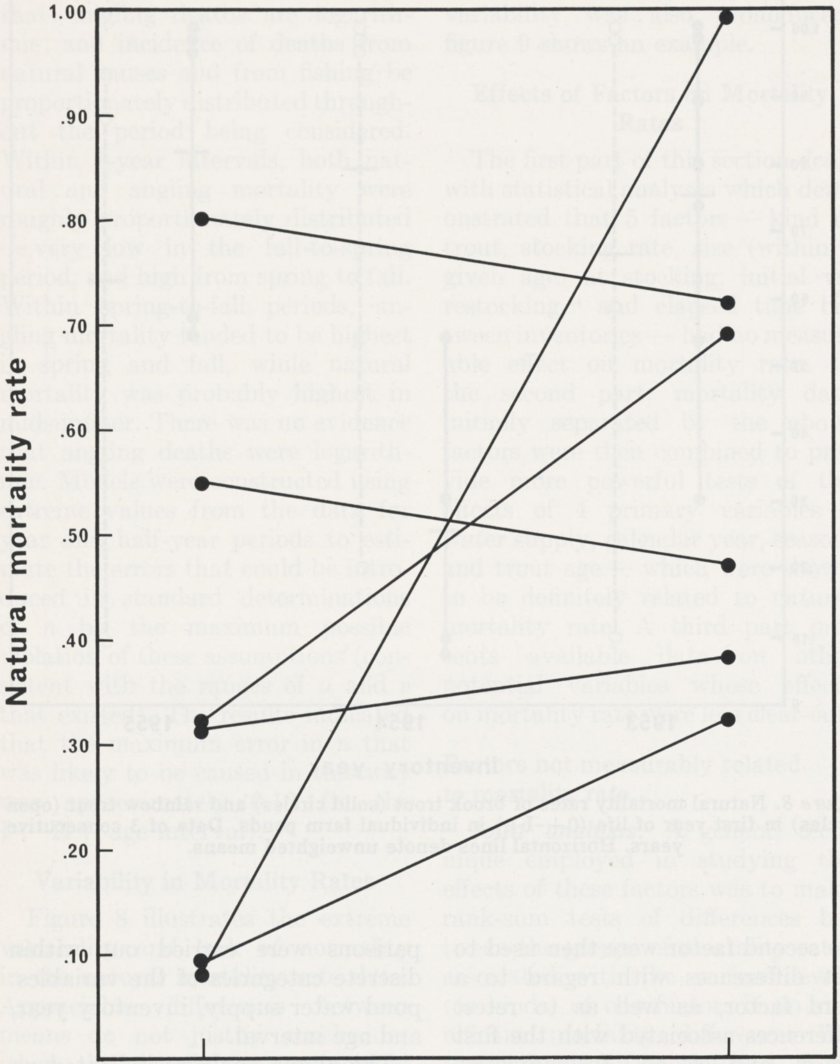

Figure 9. Natural mortality rates of the same populations of brook trout in the same 6 ponds in 2 consecutive 1-year periods. A given line connects the 2 observations from the same pond.

(within an age interval). Other kinds of information about the effects of these factors on mortality are given below.

Kind of trout. Saila (1952) found no indications of differential survival between brook, brown, and rainbow trout in separate ponds. He also determined that average survival from age 0–I was the same for all 3 species when stocked in equal numbers in each of 3 ponds.

The present study afforded 10 within-pond comparisons between 2 kinds of trout of the same age in the same time period. Various age intervals (up to III+) and combinations of the 3 kinds used were represented. In 6 of these comparisons natural mortality rates of both kinds of trout were identical, in the remaining 4 ponds differences were slight, inconsistent, and nonsignificant as tested by chi-square.

In July 1955, unprecedented and atypically high water temperatures produced complete kills in 70 percent of the 37 experimental ponds that had contained trout in the spring. Among these ponds in which bottom temperatures during the kill period exceeded 74°F., equal percentages of complete kills occurred in ponds containing each kind of trout. Frequent observations were made on all ponds while the kills were in progress. In 8 of the ponds with more than 1 kind of trout, there was no evidence of species differences in resistance to high temperature. Even in normal summers, small differences in temperature tolerance between different kinds of trout would rarely be expected to produce differential mortality in these farm ponds, where marked temperature fluctuations during summer months are characteristic.

Observations on comparative longevity of the 3 kinds of trout were limited by the 1955 kills described above. Brook and rainbow trout each survived to age III in 45 percent of 9 and 7 ponds, respectively, stocked in 1952. In the entire body of data, brook trout survived to age IV in 3 out of 132 ponds; rainbow trout attained the same age in 2 of 45 ponds.

Stocking rate. In the first summer following stocking, there were no consistent or significant mortality differences between groups of ponds stocked with spring fingerlings at low (100–400/acre) and at high (401–1000/acre) rates, in 3 available group comparisons. The same was true in 3 group comparisons of the 0+–I+ mortality of fall fingerlings at initial population densities of 100–400 and 401–800 per acre. Sometimes class mean natural mortality rates for groups of ponds stocked at high and low rates were virtually identical. Natural mortality rate was equally unrelated to the poundage of fish stocked, or for that matter, to the poundage present at the beginning of any age interval.

Size when stocked. There were no mortality differences associated with initial size in the first summer after stocking as spring fingerlings, but initial size differences in this group were not large, and the number of available comparisons limited. Among fall fingerling plantings of 2 initial size categories — 4.1–4.4

inches vs. 6.3–8.4 inches — 4 comparisons involving a total of 17 ponds were available. There were no size-associated mortality differences in either the first half year or year following stocking. In some respects farm ponds do not afford very rigorous tests of trout survival potential. Perhaps the initial size differences tested here would have influenced mortality rates of fall fingerlings in other habitats.

Initial stockings vs. restockings. Table 11 gives overall mean natural mortality rates of initially stocked and restocked trout in the first half year and year following stocking as spring fingerlings and as fall fingerlings. Although there are errors inherent in combining mortality data from different years and water supply categories in this way, the distribution of these particular data with respect to those variables was not such as to produce any serious bias in this case, and the table gives a reasonable picture of the kinds of relationships that were found in each year and water supply category that afforded comparisons. Mortality of spring fingerlings in the first 5 or 6 months following stocking was significantly higher in ponds containing older holdover fish from earlier plants, presumably due to predation. These differences also affected spring fingerling mortality rates computed for the whole year following stocking, although the presence of older trout did not, apparently, affect mortality of the spring fingerlings in the second half of that year. Mortality of fall fingerlings, on the other hand, did not differ measurably between ponds with and without holdover fish. These conclusions were supported by rank-sum tests of mortality differences between groups of ponds within discrete water supply and calendar year categories.

The much lower average mortality of all fall fingerlings, compared with all spring fingerlings, in the first half year following stocking was presumably associated with seasonal mortality differences, which were usually substantial in all age

Table 11. **Natural mortality rates of spring and fall fingerling trout 1/2 and 1 year after stocking in farm ponds***

Stock	Elapsed time since stocking			
	5–6 months		11–12 months	
	Initial	Restock	Initial	Restock
Spring fingerlings	65	85	75	90
	(summer period)			
Fall fingerlings	25	25	70	65
	(winter period)			

* Unweighted means for (1) initial plantings, and (2) restockings where older fish were present. Combined data for spring-fed and runoff ponds in all years.

groups.[15] The available data on spring fingerlings did not indicate whether one species of holdover trout was more predaceous than another. In all age intervals beyond 0+, mortality rates of trout stocked as spring fingerlings did not differ from those stocked as fall fingerlings.

Elapsed time between inventories. Within each age interval, in each calendar year and pond water supply category, there was no suggestion of any relationship between elapsed time (to the nearest 0.1 month) and natural mortality rate. In the data for any given age interval, the range in time intervals between population inventories seldom exceeded 6 weeks; the small differences in mortality rate measurements that were presumably associated with this variation were completely masked by the much larger sources of variation described in the next section.

Primary variables

Pond water supply. Mean natural mortality rates in spring-fed and runoff ponds, by age intervals and inventory years, are given in table 12. Only data based on more than 1 pond are shown. In most "summer" periods (0–0+, I–I+), and in all whole-year intervals but 1, mortality rates averaged higher in runoff ponds — significantly so in 2 cases, as judged by rank-sum tests between comparable groups. Mortality rates in the 2 categories of ponds did not differ significantly in any of the "winter" comparisons (0+–I). The data in table 12 suggest that mortality differences between spring-fed and runoff ponds tended to be less in exceptionally cool summers (1954, when conditions in runoff ponds were unusually favorable), or in exceptionally hot summers (1955, when conditions in spring-fed ponds were exceptionally unfavorable); greater mortality differences were observed in summers (1952 and 1953) when temperatures were intermediate. The very high mortality means for the 0–I age interval were produced by the heavy mortality of spring fingerlings in the 0–0+ period.

Season. The half-year means for 1953 and 1954 in table 12 show that mortality rates in either spring-fed or runoff ponds were generally higher in summer than in winter. Seasonal variation in mean mortality rate was greater in the runoff ponds, where summer conditions were more marginal. Mortality data from individual ponds that were inventoried at successive half-year intervals also showed seasonal fluctuations.

Calendar year. Rank-sum tests using mortality data within a given age interval and pond water supply category revealed numerous significant differences between years. Figure 10 shows mean natural mortality rates of 3 age groups of trout in 3 consecutive years, in spring-fed and in runoff ponds (data in table 12), together with total solar radia-

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[15] Flick and Webster (1964) found that in Adirondack ponds, where water temperatures were always below 65°F., first-summer mortality of spring fingerling brook trout approximated the comparable average determined in the present study. While the 2 types of environments differed in many other respects, this nevertheless suggests the possibility that factors other than high water temperatures could have played a part in the observed first-summer mortality in central New York farm ponds.

Table 12. **Mean natural mortality rates in spring-fed (S) and runoff (R) ponds, by age intervals and inventory years**

(Combined data for brook trout, rainbow trout, and brook × brown trout hybrids. Numbers of ponds in parentheses. Data for a single pond in a category are not included.)

Inventory year	Half-year age intervals										Whole-year age intervals									
	0–0+ (Summer)		0+–I (Winter)		I–I+ (Summer)		I+–II (Winter)		II–II+ (Summer)		0–I		0+–I+		I–II		I+–II+		II+–III+	
	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R	S	R
1952	34 *(3)*	88 *(9)*																		
1953	59 *(4)*	97 *(2)*	51 *(3)*	17 *(4)*		85 *(3)*					68 *(3)*	90 *(5)*	53 *(8)*	76 *(13)*			76 *(2)*			
1954	58 *(6)*	66 *(5)*	24 *(2)*	12 *(2)*	13 *(2)*	47 *(3)*					69 *(2)*	97 *(2)*	34 *(4)*	40 *(4)*			54 *(5)*	49 *(5)*		
1955												98 *(2)*	84 *(13)*	94 *(10)*			86 *(2)*	100 *(5)*	99 *(5)*	99 *(3)*
1956			26 *(5)*	7 *(4)*			37 *(4)*									70 *(2)*				
1957	74 *(4)*		21 *(3)*						54 *(2)*											
1958			74 *(2)*								94 *(2)*									

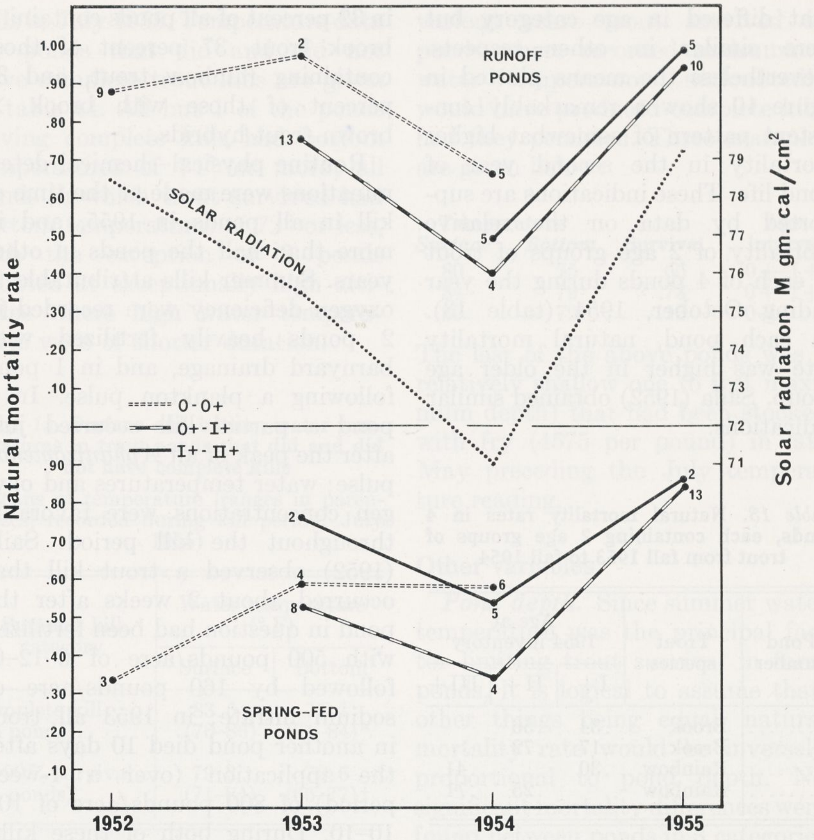

***Figure 10.* Solar radiation and mean natural mortality rates of 3 age groups of farm pond trout during 3 consecutive years, in spring-fed and runoff ponds. Data from table 12. Numbers of ponds shown beside points.**

tion for the period May through September recorded at Ithaca in the same years. These data show a marked similarity between annual mortality trends in different age groups and pond water supply categories. The correlation between mean mortality rate and solar radiation was equally pronounced in the years 1953–55; in 1952, the effects of high solar radiation were presumably offset by those of precipitation, which was heaviest in that year. Over the 4-year period, mean mortality rates were much more closely correlated with solar radiation, than with mean air temperature or total precipitation during the May–September period.

Age of trout. Rank-sum tests indicated no significant mortality differences, in the 4 available comparisons, between groups of ponds that differed in age category but were similar in other respects. Nevertheless the means plotted in figure 10 show a remarkably consistent pattern of somewhat higher mortality in the second year of pond life. These indications are supported by data on the relative mortality of 2 age groups of trout in each of 4 ponds during the year ending October, 1954 (table 13). In each pond, natural mortality rate was higher in the older age group. Saila (1952) obtained similar indications.

Table 13. **Natural mortality rates in 4 ponds, each containing 2 age groups of trout from fall 1953 to fall 1954**

Pond number	Trout species	Age at 1954 inventory		
		I+	II+	III+
16.......	Brook	.34	.56	
46.......	Brook	.17	.72	
35.......	Rainbow	.30		.41
30.......	Rainbow		.25	.71

Kills; temperature effects. An average of 35 different ponds were under investigation in each of the years 1952 through 1957, during which period complete kills occurred in a total of 52 ponds — 26 in July 1955.[16] Eighty percent of all kills occurred in runoff ponds; 20 percent in spring-fed ponds. Four kills occurred in winter; the remainder in the summer. Kills were recorded in 39 percent of all ponds containing brook trout, 37 percent of those containing rainbow trout, and 38 percent of those with brook × brown trout hybrids.

Routine physical–chemical determinations were made at the time of kill in all ponds in 1955, and in more than half the ponds in other years. Summer kills attributable to oxygen deficiency were recorded in 2 ponds heavily fertilized with barnyard drainage, and in 1 pond following a plankton pulse. In 1 pond a partial kill occurred just after the peak of an *Aphanizomenon* pulse; water temperatures and oxygen concentrations were favorable throughout the kill period. Saila (1952) observed a trout kill that occurred about 2 weeks after the pond in question had been fertilized with 500 pounds/acre of 6–12–6; followed by 160 pounds/acre of sodium nitrate; in 1953 all trout in another pond died 10 days after the application (over a 1-week period) of 800 pounds/acre of 10–10–10. During both of these kills, temperature and oxygen in surface and bottom waters were optimum. On the other hand, in 2 ponds fertilized in mid-June, one with 500 pounds/acre of 8–8–4, the other with 1000 pounds/acre of 6–12–6, spring-to-fall natural mortality rates were 0.16 and 0.30, respectively.

Virtually all other kills were attributable to high water temperature. Bottom water temperatures that were recorded during these kills ranged from 75° to 83° F. The most detailed information on relationships between trout kills and water temperatures is that obtained from 37 ponds during the extensive

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[16] In this summer, mean June–August water temperature 20 feet below the surface of the Ithaca City Reservoir attained a maximum for the 30 consecutive years covered by temperature records – an indication of how unusually severe conditions were.

kills in July 1955. Temperature data for ponds that did and did not have complete trout kills are given in table 14. All but 1 of the ponds having complete kills had bottom temperatures of 74° or more; all ponds in which trout survived had bottom temperatures of 72° or less, with the exception of 3 ponds situated at exceptionally high altitudes where high water temperatures were of shorter duration.

Table 14. **Surface and bottom water temperatures in trout ponds that did and did not have complete kills**

(Means of temperature [ranges in parentheses] recorded during kill period, July 1955)

Summer kill category	Water temperature (° F)	
	Surface	Bottom
Complete kill..... (26 ponds).......	83.5 (76–86)	77.1 (71–84)*
15–90% survival.. (11 ponds).......	79.3 (71–84)	72.6 (66–77)†

* 74° or above in all but 1 pond.
† Below 73° in all but 3 hill-top ponds.

These and other temperature data obtained in this period suggest that heat death of trout in ponds was not simply a function of the maximum temperature attained, but also of the duration of temperatures in excess of about 73°. In 1 pond where daily observations were made, bottom water temperatures remained between 73° and 74° from July 9 through 25. No dead or distressed trout were observed until July 19, but apparently all of the trout died the next 7 days. In various years trout survived in ponds where recorded midsummer water temperatures undoubtedly would have produced complete kills had they persisted. Three examples are given below:

Temperature		Survival	Age interval
Surface	*Bottom*		
80	75	.66	0+–I+
84	79	.73	0+–I+
89	79	.12	0–I

The last of the above ponds was a relatively shallow one (6 feet maximum depth) that had been stocked with fry (4575 per pound) in late May preceding the July temperature reading.

Other variables

Pond depth. Since summer water temperature was the principal factor limiting trout survival in farm ponds, it is logical to assume that, other things being equal, natural mortality rate would be inversely proportional to pond depth. No significant mortality differences were found between ponds in 3 categories of maximum depth (5–6, 7–9, and 10–14 feet) that were comparable with regard to age interval, inventory year, and water supply. However, the available comparisons were limited in number, and further by the fact that the large majority of ponds were in the 7- to 9-foot depth category. There was a tendency for mortality means to vary inversely with means of maximum pond depth.

Pond elevation. Although there were some indications in the summer kill data (table 14) that pond elevation may have influenced survival, there were no significant differences between mortality rates in groups of ponds (subdivided as above) at elevations of 400 to 1199 feet and those at 1200 to 1999 feet. Mortality means tended to be inversely related to elevation in the 10 available comparisons, 7 of which involved whole-year age intervals. Whole-year data may be unsuitable for measuring elevation effects because, in this climate, higher elevation may possibly decrease mortality in summer but increase it in winter.

Escape. In 1 spring-fed pond with no trickle tube and another with an inadequate one, from 10 to 20 trout escaped (subsequently recovered) on occasions when excess water flowed out through the emergency spillway. Such phenomena would be more likely to occur in spring-fed ponds, which have a larger water supply than runoff ponds (given the same average watershed area), and more likely in the late fall and early spring, when runoff is maximal. This might account for the (nonsignificantly) higher mean mortality rate in spring-fed than in runoff ponds during the fall-to-spring period in 3 different years (0+–I, table 12).

Predators. The most serious potential fish predator in typical farm ponds in this region appeared to be the domestic muscovy duck, *Cairina moschata*. On 2 occasions these ducks were observed gorging themselves on 2- to 3-inch bluegills. In each of 2 spring-fed farm ponds in different localities, the only time when trout mortality was not outstandingly low was the summer of 1954 (a relatively cool one), when groups of muscovies were present and when 0–0+ mortality rates were 0.88 in one pond, 0.98 in the other. Great blue herons (*Ardea herodias*) were not uncommon visitors to more isolated ponds, and in 4 pond inventories some of the yearling trout seined had characteristic puncture wounds in the dorsum, just in front of the dorsal fin. However, no evidence of excessive mortality attributable to heron predation was obtained in the course of this study. Kingfishers (*Megaceryle a. alcyon*) nearly eliminated a population of spring fingerling trout in a remote spring-fed pond located in woods. The birds' feeding activities were observed regularly by the pond owner, and the extent of their depradation (n = 0.94, 0–0+) was established by population inventory. However, kingfishers did not appear to frequent most of the farm ponds, which were typically located in open fields.

Combined Mortality Data

For determining standing crops of trout at various ages in the "average" farm pond, the mean natural mortality rate for a given age interval was computed in the following manner: (1) The mean mortality rate of a particular calendar year was determined by summing all individual pond mortalities in that year (and age interval) — regardless of species, age at stocking, or pond water supply — and dividing by the number of ponds. This was done because the larger variation between individual ponds, relative to variation associated with pond water supply, indicated that the most valid procedure was to give equal weight to each pond to obtain that mean (for a given year) which had the greatest predictive value. (2) The overall mean mortality rate for the age interval was taken as the unweighted average of the means for all calendar years. The great variation in mortality rate with calendar year made it essential to give equal weight to the mean for each year. For the same reason, Saila's means for each age interval were treated as those of any other year in computing the overall mean natural mortality rates.

The mean mortality rates are given in table 15. Mortality relationships between seasons and age groups agree with those indicated in the previous section. The bottom row of table 15 gives "means" synthesized from combinations of the appropriate actual means. Actual means (upper row of table) were used in subsequent determinations of standing crop. Synthesized means, which served only as indicators of the validity of actual means, were computed in the manner described below.

Ricker (1958, p. 25) shows that the relationship of total mortality rate (a) to 2 component mortality rates, such as rates of fishing (m) and natural (n) mortality is

$$a = m + n - mn \qquad (1)$$

Analogously, the relationship between natural mortality rate for a whole year (n) and the natural mortality rates in the first (n_1) and second (n_2) parts of that year is

$$n = n_1 + n_2 - n_1 n_2 \qquad (2)$$

Hence, if the relationships between half-year and whole-year actual means in table 15 are as expected, provided discrepancies in the data that produced them were not too great, the actual mean n for the age interval 0–I should be approximated by the sum of the actual means for 0–0+ (0.75) and 0+–I (0.30) minus their product. The synthesized mean for 0–I, then, is

$$.75 + .30 - (.75)(.30) = 0.825$$

which closely approximates the actual mean of 0.80.[17]

Table 15. **Overall mean natural mortality rates of trout in half-year and whole-year intervals of farm pond life**

(Data are unweighted averages of simple means for individual years in period 1949–58, inclusive, rounded to nearest 0.05, with number of ponds in parentheses. Synthesized "means," computed from combinations of appropriate whole-year and/or half-year actual means, included for comparison)

Item	Half years					Whole years				
	0 0+	0+ I	I I+	I+ II	II II+	0 I	0+ I+	I II	I+ II+	II+ III+
Mean	.75 (44)	.30 (31)	.45 (13)	.50 (9)	.60 (3)	.80 (20)	.60 (61)	.75 (7)	.80 (20)	.80 (10)
Synthesized mean	.714	.273	.500	.500	.600	.825	.615	.725	.800	..

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[17] In terms of survival, $s_1 s_2 = s$, or (.25) (.70) = 0.175 $\cong$ 0.20.

Carrying this process a step further, a half-year mean (*e.g.* that for 0–0+) can be synthesized from actual means for a whole-year (0–I) and half-year (0+–I) interval, by changing the appearance of formula (2) as follows:

$$n = n_2 + n_1(1 - n_2),$$

whence

$$n_1 = \frac{n - n_2}{1 - n_2} \quad (3)$$

Thus the synthesized mean for 0–0+ using actual means for 0–I (n) and 0+–I (n_2) is

$$\frac{.80 - .30}{1.00 - .30} = 0.714,$$

which is reasonably close to the actual mean of 0.75. This method was used to produce all the synthetic means for half-year intervals up to the last (II–II+), where one runs out of n_2's. However, formula (3) can be modified to read

$$n_2 = \frac{n - n_1}{1 - n_1}$$

and this formula used to determine the synthetic mean for II–II+ from actual means for I+–II+ (n) and I+–II (n_1) as

$$\frac{.80 - .50}{1.00 - .50} = 0.60,$$

which happens to be identical with the actual mean for the II–II+ interval. The fact that there is uniformly close agreement between actual and synthesized means in table 15 is more surprising than it might appear, because the majority of whole-year data from individual ponds were not comprised of consecutive pairs of component half-year data from these same ponds.

Fishing, Catch and Effort

Fishing Patterns

In the collective data from 73 ponds where owners recorded the time of day fished, 60 percent of all fishing was done between 5 and 8 p.m.; 19 percent between 2 and 5 p.m. The monthly distribution of total fishing effort was very similar in each year of the study. Averaging the data from various years, 20 percent of a year's fishing trips were made in each of the months April, May, and June; however, percentages of the total year's fishing hours reached a sharp peak in May (37 percent). Other statistics of fishing effort are as follows:

Item	Mean	Range
Fishing trips/year	6.4[18]	0–18
Hours/trip	1.4	0.2–3.6
Anglers/trip	2	1–5
Angler hours/pond/year	17.8[19]	0.5–63.5

The number of fishing trips or angler hours in a year was independent of pond size — ponds were fished by the unit, not by the acre. Multiplying the average number of angler hours in a year (17.8) by the estimated number of New York farm ponds stocked with trout (4000 in 1960) gives an estimate of

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[18] Poisson distribution.

[19] Computed independently, from pond angling records.

71,200 hours of fishing per year in these ponds. Multiplying this figure by the average catch per hour in this study (unweighted mean of brook and rainbow trout catch rates — 2.6 fish per hour) indicates that New York farm ponds provide a total catch of about 185,000 trout per year.

Most of the ponds could have been harvested much more intensively; average rate of exploitation was 0.22. One pond owner harvested 90 (45%) of 200 yearling brook trout in a May–June period.

Catch per Hour

By far the most potent source of variation in this statistic was the individual fisherman. Variation in catch rate between fishermen was so large (from 0 to 16 trout per hour) that it masked the effects of most other variables in large-scale analyses of between-pond data. For this reason, within-pond data provided the only useful information on some of these effects, which are discussed below.

Population density and age

Catch data were available from 9 ponds, each containing known numbers of age I and II brook trout, and 4 with known numbers of age I and II rainbow trout. In all but 2 of these ponds, the numbers of both age groups caught did not differ significantly (by chi-square) from the catches to be expected from their relative population densities. Two-year-old trout were significantly more vulnerable to angling in 1 brook-trout and 1 rainbow-trout pond. Although markedly higher vulnerability of 2-year-olds has been reported a number of times (Anonymous, 1952; Hunt, *et al.*, 1962; and Mullan, 1956, among others), farm pond catches appeared to be usually dependent on population density and not on age, in comparisons where variations due to species differences and angler differences were eliminated.

Time of day; calendar year

Suitable within-pond data were not available to test the effects of these variables on angling success. In various possible combinations of between-pond data, there was no evidence that catch rate varied with year or time of day, although there seems little doubt that at least the latter variable would influence trout-pond catch rate in controlled experiments.

Kind of trout; month

Effects of these 2 variables on catch rate were so pronounced as to be detectable in the highly variable between-pond data. The relationships were similar in each year, so data from all years were used to compute mean monthly catch per hour of the 3 kinds of trout shown in figure 11. Exact positions and shapes of these lines probably are of no significance, but their relative positions and the overall seasonal trend in catch rate are apparently valid.

Buss (1956) and Webster (personal communication) also have noted the greater vulnerability of brook × brown trout hybrids. Statistically significant species differences paralleling those shown in

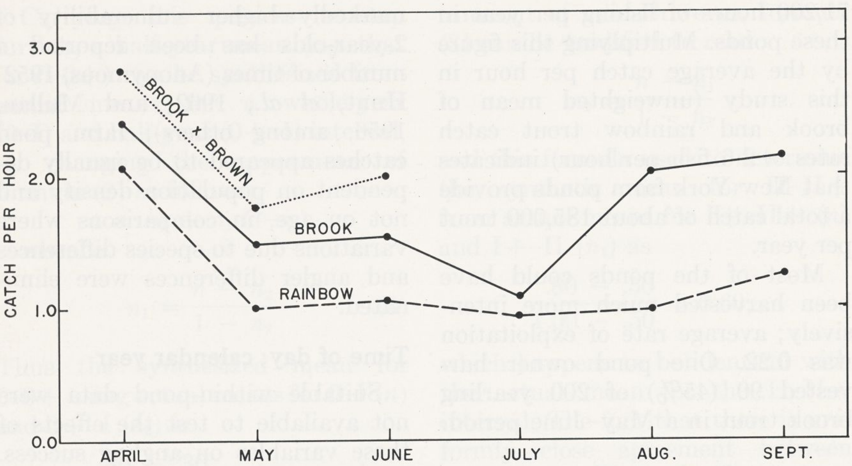

Figure 11. **Unweighted mean catch per hour of brook trout, rainbow trout, and brook × brown trout hybrids, by months. Combined data from the years 1952–58, inclusive.**

figure 11 were also observed in the angling data from 3 ponds in this study containing more than one kind of trout of the same age, and in 3 similar tests by Saila (1952).

Winter fishing

Fishing through the ice was done in 2 ponds between late January and early March, using artificial lures and natural baits with equal success. In a total of 6 trips (41 angler hours), catch per hour ranged from 0.7 to 3.7. In 1 pond with about 500 age I brook trout and 100 age III rainbow trout, catches of both species were proportional to their population numbers in 3 trips; in a fourth trip, 4 men caught 10 brook trout and no rainbow trout in 40 minutes' fishing. In the other pond, 6 anglers in 1 hour caught 20 of the approximately 90 age II brook trout present.

Standing Crop

Determinations

Numbers and pounds of trout per acre to be expected at successive ages from 3 different stocking rates in the average unfished pond, were calculated using the mean growth and natural mortality data of tables 10 and 15. The results are given in table 16; data from the last 2 columns of this table are graphed in figure 12. These standing crops are well within the ranges of empirical data.

The pounds of trout per acre in an unfished population at an age t (W_t) may also be calculated from the poundage present at the preceding age (W_o) and the coefficients

Table 16. **Determinations of average number/acre (*N*) and pounds/acre (*W*) of farm pond trout at various ages, applying mean growth and mortality data of tables 10 and 15 to 3 stocking rates**

Age	s*	w	N	W	N	W	N	W
0		.004	800	3	1600	6	2400	10
	.25							
0+		.07	200	14	400	28	600	42
	.70							
I		.23	140	32	280	64	420	97
	.55							
I+		.50	77	38	154	77	231	115
	.50							
II		.65	38	25	77	50	115	75
	.40							
II+		.89	15	13	31	28	46	41
	.20							
III+†		1.35	3	4	6	8	9	12

* Survival = 1.00 minus the appropriate value of n from table 15.
† No data for age III.

of mean growth ($\bar{g}$, table 10) and natural mortality ($\bar{q}$ from corresponding mean n values in table 15) for the half-year age interval o to t, using the formula

$$W_t = W_o \times e^{\bar{g}-\bar{q}}$$

(Ricker, 1958, p. 31)

The same results were obtained by either computational method. Coefficients of mean trout growth and natural mortality in each half year of pond life are plotted in figure 13. Seasonal effects are apparent. A population attains its maximum biomass at the time when coefficients of growth and mortality are equal (Ricker, 1958, pp. 210–211). This point ($\bar{g} = \bar{q}$), where the 2 lines cross in figure 13, exactly corresponds (in population age) to the point of maximum biomass indicated by a solid arrow in figure 12.

Evaluation of Method Used

In these trout pond data, average standing crops in unfished populations computed from average growth and mortality rates are considered much more reliable than means of actual standing crops observed. The latter were functions not only of growth and mortality in a particular pond, but also of number stocked, and number removed by angling (some of which would otherwise have survived). Another important reason for working with mean growth and mortality rates was that doing so more than doubled the number of ponds on which standing crop determinations could be based, relative to the number available for means of observed standing crops. This was because many ponds for which valid growth determinations (including data on weight increments) were available did not have correspond-

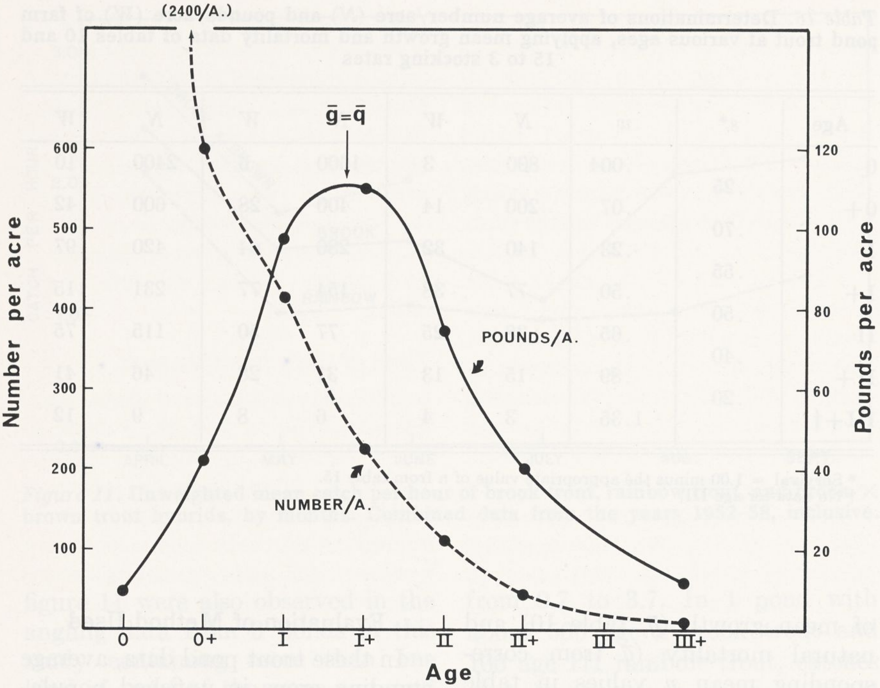

Figure 12. **Standing crops of trout at various ages in the "average" unfished New York farm pond stocked with 2400 spring fingerlings, per acre. Data from last 2 columns of table 16. Undulations in number per acre are caused by seasonal changes in mortality rate. Large arrow indicates age at which biomass is maximal, and corresponds to age at which (in figure 13) coefficients of mean growth ($\bar{g}$) and natural mortality ($\bar{q}$) are equal.**

ing valid mortality determinations, and *vice versa*.

It appears that the standing crops for a planting of 600 fall fingerlings per acre (or 2400 spring fingerlings, with average survival) shown in table 16 and figure 12 are reasonable approximations of averages that might be expected from this stocking rate. Mean population densities associated with the growth data of figure 5 are comparable with those that would prevail in corresponding age intervals of average populations (table 16) stocked with 600 fall fingerlings per acre, as shown below:

Age interval	Mean population density in growth data	Mean population density at 600/acre stocking
0+–I+	306	393
I+–II+	156	115

The mean population density that would prevail in the first year of pond life after stocking at 600/acre is somewhat higher than that which characterized the growth data for that age interval, and for which density data are available.[20] But

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[20] There is no evidence that the combined growth data used to obtain the means in table 10 were characterized by a different mean or range in population density than were the data shown in figure 5, for which density data were available.

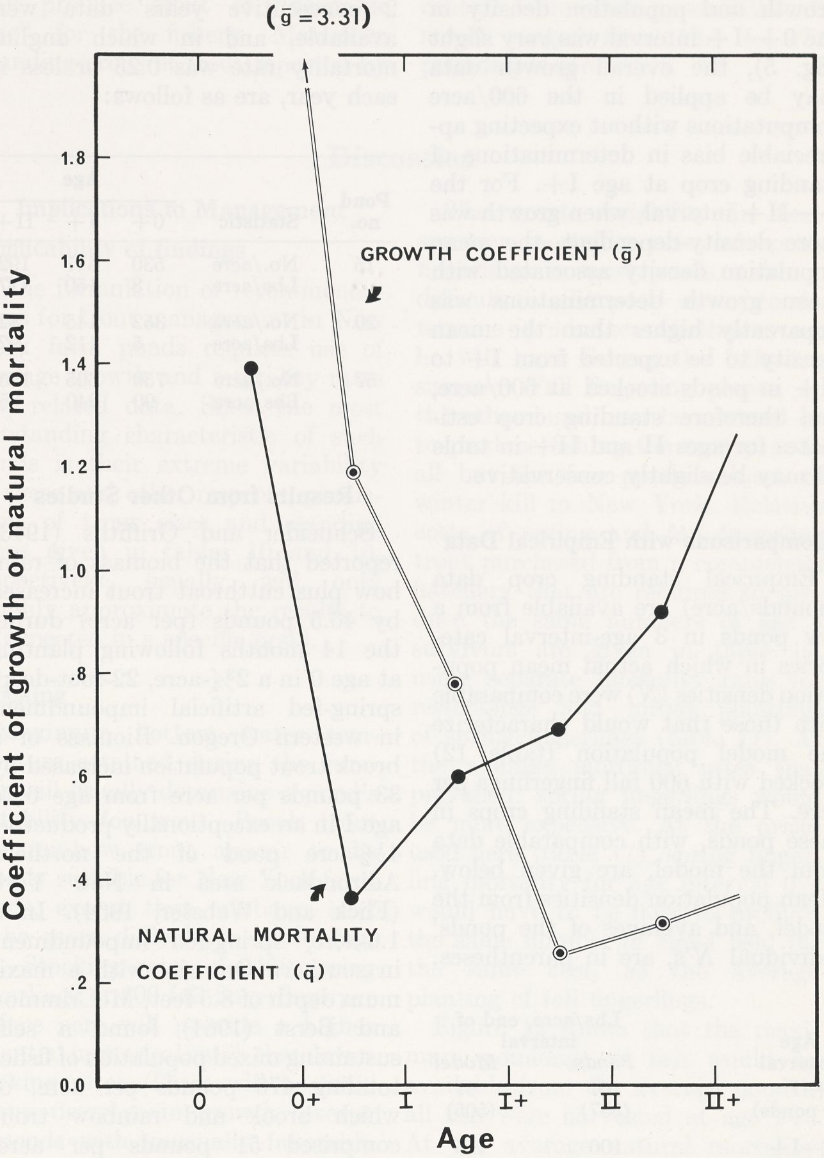

Figure 13. Growth coefficients (from table 10) and natural mortality coefficients (for values of *n* in table 15) of trout in half-year age intervals of farm pond life.

because the relationship between growth and population density in the 0+–I+ interval was very slight (fig. 5), the overall growth data may be applied in the 600/acre computations without expecting appreciable bias in determinations of standing crop at age I+. For the I+–II+ interval, when growth was more density-dependent, the mean population density associated with mean growth determinations was apparently higher than the mean density to be expected from I+ to II+ in ponds stocked at 600/acre, and therefore standing crop estimates for ages II and II+ in table 16 may be slightly conservative.

Comparisons with Empirical Data

Empirical standing crop data (pounds/acre) are available from a few ponds in 3 age-interval categories in which actual mean population densities ($\bar{N}$) were comparable with those that would characterize the model population (table 12) stocked with 600 fall fingerlings per acre. The mean standing crops in these ponds, with comparable data from the model, are given below. Mean population densities from the model, and averages of the ponds' individual $\bar{N}$'s, are in parentheses.

Age interval	Lbs/acre, end of interval *Ponds*	*Model*
0+–I (5 ponds)	107 (537)	97 (505)
0+–I+ (6 ponds)	106 (430)	115 (393)
I+–II+ (6 ponds)	67 (127)	41 (115)

Numbers and pounds of trout per acre at 3 ages in 3 ponds from which 2 consecutive years' data were available, and in which angling mortality rate was 0.25 or less in each year, are as follows:

Pond no.	Statistic	Age 0+	I+	II+
15	No./acre	530	417	192
	Lbs/acre	8	150	117
20	No./acre	352	145	82
	Lbs/acre	5	112	92
57	No./acre	750	665	150
	Lbs/acre	90	240	65

Results from Other Studies

Schneider and Griffiths (1943) reported that the biomass of rainbow plus cutthroat trout increased by 46.5 pounds (per acre) during the 14 months following planting at age 0 in a 2¾-acre, 22-foot-deep, spring-fed artificial impoundment in western Oregon. Biomass of a brook trout population increased by 33 pounds per acre from age 0 to age I in an exceptionally productive 4½-acre pond of the northern Adirondack area in New York (Flick and Webster, 1964). In a 1.6-acre, spring-fed impoundment in southern Ontario, with a maximum depth of 8.5 feet, McCrimmon and Berst (1961) found a self-sustaining mixed population of fishes totaling 476 pounds per acre, of which brook and rainbow trout comprised 51 pounds per acre. Johnson and Hasler (1954) estimated 50 pounds per acre as the average standing crop of rainbow trout that could be maintained in three 3- to 6-acre dystrophic lakes of upper Michigan–Wisconsin and still produce trout of "desirable size" for the fishery. Maximum standing crops of trout reported by Hatch and Webster (1961) in 4 central Adirondack ponds (12 to 42 acres) ranged from 12.5 to 17.9 pounds per acre.

Discussion

Implications to Management

Applicability of findings

The formulation of recommendations for trout management in New York farm ponds requires use of average growth and mortality rates and related data. Since the most outstanding characteristic of such ponds is their extreme variability in these and other respects, predictions of trout sizes and standing crops given in tables 10 and 16, respectively, usually will only roughly approximate the results to be expected in a specific pond.

Stocking

Maximum bottom water temperature attained during the summer will usually determine a pond's suitability for trout. Brook trout and rainbow trout appear to be equally suitable for New York farm ponds, except that rainbows tend to be more difficult to catch (fig. 11). Stocking rates of 2400 spring fingerlings or 600 fall fingerlings per surface acre will provide a higher potential numerical catch than lower stocking rates. There will be little if any decrease in growth, except in ponds with unusually favorable summer temperatures and no holdover fish present, where the rate of 2400 spring fingerlings might give a large enough population of age I fish to produce stunting.

The great variability in first-summer mortality rates of spring fingerlings in most ponds makes it difficult for the pond owner to determine in advance whether or not he will have fishing the following summer. Fall fingerling plants, on the other hand, can be counted on to produce fishing the next year in all but the few ponds subject to winter kill in New York. Relative costs of spring and fall fingerling trout purchased from a commercial hatchery that are required to produce the same numbers of age I survivors are given in table 17, using separate mortality rates for restockings and initial plantings of spring fingerlings (table 11). At the average mortality rates that prevailed, spring fingerlings would be more expensive. At the prices used here (table 17), spring fingerling mortality for age interval 0–I would have to be 0.68 to produce the same number of age I fish, for the same cost, as the average planting of fall fingerlings.

Figure 12 shows that the maximum poundage of fish would be available from the average pond if all fish were harvested at age I+. At the average natural mortality rates of this study, the loss in potential total harvest (numbers or pounds) resulting from failure to harvest a substantial portion of the fish population in the first year

Table 17. **Comparison of numbers, pounds, and costs of spring and fall fingerling trout required to produce equal numbers of age I fish in average New York farm pond**

Stock	Stocked			Present at age I	
	Plant	Number	Cost*	Number	Pounds
Fall fingerlings	Initial or Restock	600	$190.	420	97
Spring fingerlings	Initial	1,680	$240.	420	115
	Restock	4,200	$610.	420	115

* From prices quoted by members of American Fish Culturists' Assoc. Prices at western hatcheries apparently are lower (personal communication, A. E. Borell).

would be large. At average exploitation rates found in this study, 2 to 3 times as many trout (and about 50 percent more pounds) would be harvested in 2 summers (I–I+ and II–II+) as could be harvested in the second summer alone. Apparently yields also can be easily increased by fishing in winter months. To maintain satisfactory fishing, most ponds must be restocked every other year; fall fingerlings are much more economical for this purpose.

Conduct and Design of Experiments

These studies have led to certain conclusions about experimental conduct and design that may be useful to others contemplating similar investigations. These suggestions stem primarily from the inherent variability between ponds.

Conduct

Half-year data are more than twice as valuable as whole-year data, and ponds should be inventoried in early spring and late fall, within the shortest possible period in the same months each year. The 2 inventory months should bisect the calendar year; probably April and October would be best in climates such as New York's. About 2 months before fall inventories, each experimental pond should be checked to determine if weeds need be controlled in order to permit inventory. Chemical weed control should be conducted 7 or 8 weeks before inventory; mechanical control (assuming the weeds will be removed from the pond), about 2 weeks before.

When ponds are inventoried, all fish obtained in a recapture seine haul should be accurately weighed as well as measured, using an anaesthetic if necessary. As shown earlier, weight is a more useful growth index than length in certain respects.

Within the categories of information sought, every effort should be made to insure that the fish stocked in different years are uniform with regard to species, genetic constitution, hatchery source and rearing conditions, stocking rate, and initial size and weight.

Experimental ponds should be as uniform as possible with regard to morphometry, size, soil type, elevation, geographic location, watershed size, and watershed use.[21] Ponds in remote locations are vulnerable to poaching, unauthorized stocking, draining, and other "accidents", and should not be used for experiments. Ideally, only those ponds over which complete control can be exercised at all times should be used for experiments in fish population ecology. Only ponds of proven water-holding capacity should be selected for experiments; recently-constructed ponds should be avoided.

Design

The importance of designing an experiment with a precisely defined, discrete, rigidly delimited objective cannot be overemphasized. The temptation to incorporate deviations from the original design and/or procedure so as to "pick up accessory information" should be resisted. The experiment should be designed to obtain information on a specific question, and the design should provide the maximum uniformity possible regarding variables other than those to be tested. The necessity of adequate numbers of controls in the design is beyond question.

Maximum possible use should be made of within-pond tests. As shown in this study, for example, more information on differences in growth, natural mortality, or angling mortality between fish of different species, ages, or (within limits) initial sizes can be obtained from 5 ponds each stocked with equal numbers of each species, age, or whatever, than from 25 or more ponds, some stocked with one species or age group, and some with another.

Sample size

If the variance of a normally distributed measurement is known, the number of replicates needed to obtain estimates within a specified level of accuracy can be determined, with a given probability. Using appropriately transformed natural mortality rate data [22] (species combined), for the various years and age intervals providing sufficient data, as well as pooled variances of the several years' data in each age interval, the average numbers of spring-fed and of runoff ponds needed to detect natural mortality rate differences of 0.10 and of 0.20 between spring-fed and runoff ponds were computed for each age interval with a probability of 0.95, according to the procedure described by Snedecor (1956, pp. 94–95). These average numbers are given in table 18. To illustrate its use: The data on variability of natural mortality rates in the 0+–I+ age interval in 3 years' data from a total of 24 spring-fed and 25 runoff ponds indicates that, on the average, about 27 spring-fed ponds and 17 runoff ponds would be needed to detect a difference of 0.10 that actually existed between the mean mortality

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[21] The rigor in applying this criterion will be governed by the objects of the experiments. Results of tests of management measures, for example, would not have wide applicability if tests were conducted in a series of nearly uniform ponds.

[22] Each natural mortality rate transformed to arcsin $\sqrt{n}$.

Table 18. **Numbers of spring-fed (S) and runoff (R) ponds required to detect existing differences of 0.10 and 0.20 between mean mortality rates of spring-fed and runoff ponds***

Age interval	Pond water supply	Used for determinations		No. of ponds needed to detect difference between nat. mort. rate means of:	
		No. of ponds	No. years' data	0.10	0.20
0–0+	S	14	3	13	6
	R	22		17	8
0+–I	S	10	2	18	9
	R	7		24	11
0+–I+	S	24	3	27	13
	R	25		17	8
I+–II+	S	9	2	15	7
	R	8		2	1

* Averages of 2 or 3 years' data in each of 4 age intervals.

rates of spring-fed and runoff ponds; 13 spring-fed and 8 runoff ponds would be needed to detect an existing difference of 0.20.

The requirement of more spring-fed than runoff ponds in the 2 whole-year age intervals indicates that in whole-year periods mortality rates were more variable in the spring-fed than in runoff ponds. Part of the greater variability among spring-fed ponds is attributable to the criteria used in assigning ponds to water-supply categories: Although "spring-fed" was used to identify a pond with permanent springs extensive enough to maintain some outflow at nearly all times, this included ponds maintained by spring seepage as well as those fed by large springs; runoff ponds, on the other hand, were more environmentally uniform to the extent that all of them were fed exclusively by runoff from the surrounding watershed. Another factor that reduced the mortality variance in the runoff ponds was that most of the complete kills occurred in this group, so that the runoff pond mortality data were characterized by more clumping in the very high mortality categories.

The actual numbers of replicates indicated in table 18 probably are not too reliable because, even after transformation, the natural mortality rate data were not normally distributed. However, these values do provide an objective statistical basis for determining roughly how many ponds are needed to detect specified mortality differences when pond variability approximates that which prevailed in this study. Since growth data were less variable than mortality data, the numbers of ponds indicated in table 18 should be at least as adequate for growth determinations, if not more so.

Experience in this study indicated that it would be reasonable to allow for a 25 percent annual loss of pond data from various causes (see page 26). Under similar circumstances an investigator, having estimated the numbers of ponds he might require by calculations of the sort illustrated above, should increase these figures by at least 25 percent for determining the numbers of ponds in which he will start 1-year experiments; and by about 40 percent in the case of 2-year experiments.

Summary

Studies were conducted from 1952 through 1958 to determine the reproduction, growth, natural mortality, fishing potential, and standing crops of trout in 70 central New York farm ponds which had surface areas of 0.1 to 1.8 acres and maximum depths of 5 to 14 feet. Approximately half of the ponds had some degree of permanent spring water supply, while the remainder were fed entirely from the surrounding watershed.

The usual experimental approach was to stock trout as spring fingerlings (age 0) or fall fingerlings (age 0+) in series of ponds at stocking rates varying from 200 to 800 per acre, and to determine survival and growth in each pond in successive half or whole years by spring and/or fall population inventories. Standard inventory procedure involved seining a pond twice with a 150-foot bag seine for a Petersen population estimate; inventories of 15 ponds stocked 11 to 26 days earlier with known numbers of trout indicated that population estimates were nearly always accurate to within 10 percent. In the average pond inventory, fish actually counted comprised about 80 percent of the estimated population.

Of the 195 pond inventories from which usable data were obtained in the 7-year study, brook trout were the single or dominant species in 141, rainbow trout in 46, and brook × brown trout hybrids in 8. Fragmentary data on brook × lake trout hybrids and a wild strain of brook trout are also available. Saila (1952) had previously determined that brown trout are unsuitable for New York farm ponds because of their pronounced invulnerability to angling in these waters.

Survival of brook × brown trout hybrids from fertilized egg to free-swimming fry was approximately 17 percent. Brook × lake trout hybrids showed about 75 percent survival from egg to fry, but there was some evidence that they may be less well suited to New York farm ponds than many salmonids because of lower temperature tolerance. Wild and domestic brook trout did not differ appreciably in survival or growth in 3-year tests involving equal numbers of both strains in each of 2 ponds.

Nearly all farm ponds lacked suitable environmental conditions for successful trout reproduction,

although brook trout frequently spawned. Brook trout males were mature at age 0+ or I+; females at I+ or II+. Mature rainbow trout males were observed among fish of ages I, II, II+, III, and III+; mature females at ages II and III. Siphon egg incubators gave satisfactory hatches of eyed trout eggs in several ponds with heavy silt loads; green eggs in the same devices became smothered by silt before hatching.

Growth of a given trout pond population in a given time interval was measured by increment in mean length, increment in mean weight, and the coefficient of growth in mean weight ("instantaneous growth rate"). Weight increment was a better measure of growth than length increment or growth coefficient, in that it was less size-specific, and was somewhat more sensitive to changes in mean population density and to seasonal influences. Graphic analyses and rank-sum tests indicated that growth of brook trout, rainbow trout, and brook × brown trout hybrids grew at the same rates in these ponds, and that trout growth did not differ detectably with calendar year, nor with the water supply, soil type, size, or age of ponds within the ranges of available data. No doubt some effects that actually existed were masked in the complex of actions and interactions of numerous factors whose net result was growth data that varied widely between individual ponds. The same was true of data on natural mortality. Growth in a given time interval was inversely related to mean size of trout at the start of the interval. Growth was not related to population density or biomass at the start or end of an interval; mean population density inversely affected growth, but the relationship was very poorly defined in fish populations below age I+. Growth decreased with age of trout, and was somewhat slower in the October-to-April period than in April to October. Applying mean increments in length and weight, 5.6-inch, 0.07-pound, fall fingerling trout stocked in farm ponds at age 0+ attained an average length and weight, respectively, of 10.1 inches and 0.50 pounds at age I+; 14.2 inches and 1.35 pounds by age III+.

There were no differences in natural mortality rate (*n*) between brook, rainbow, or brook × brown hybrid trout of comparable ages. Natural mortality rate was not detectably related to the number, biomass, or size of trout present at the start of a given age interval. Mortality of spring fingerlings was extremely variable and fall fingerling plantings gave more dependable results, particularly when older fish from an earlier plant were present. Natural mortality rate varied markedly with calendar year, season, age of fish, and pond water supply. Duration of bottom water temperatures above 73°F was the factor that most influenced the natural mortality of farm pond trout in central New York. Mean natural mortality rates of trout in the first, second, and third years after stocking as fall fingerlings were 0.60, 0.80, and 0.80, respectively.

Virtually complete angling records were obtained from most ponds in all years. Catch rates varied with individual fishermen (and confounding factors) from 0 to 16 trout per hour, tended to be proportional to population density, and to be higher in spring and fall than in midsummer. Brook × brown trout hybrids were most vulnerable to angling, brook trout next, and rainbows the least vulnerable. Multiplying the average number of angler hours spent trout fishing in a New York farm pond in a year (17.8) by the estimated number of these ponds currently stocked with trout (4000) indicates that they are providing about 71,200 hours of trout fishing per year. Multiplying that figure by the average catch rate from this study (2.6 trout per hour) indicates that New York farm ponds are providing a total catch of about 185,000 trout per year. The average rate of exploitation was 0.22, and most of the ponds could have been harvested much more intensively.

Mean growth and natural mortality rates were used to determine expected standing crop in each half year of pond life, in the absence of fishing. These computations indicate that an average planting of 600 fall fingerling trout (42 pounds) per acre in an average, unfished, central New York farm pond reaches a maximum biomass of 115 pounds per acre a year later (age I+), at which time 230 ten-inch trout remain. Standing crops in the succeeding 2 years would average 46 trout (41 pounds) per acre at age II+, 9 trout (12 pounds) per acre at III+. The validity of these computed mean standing crops is supported by the empirical data; a pond stocked with 750 fall fingerling trout per acre contained 665 fish (240 pounds) per acre a year later.

Poundages of trout produced in environmentally suitable New York farm ponds compare most favorably with the limited data available from a small number of trout studies of somewhat similar environments. Because they do not permit trout reproduction, most New York farm ponds must be restocked every other year to maintain satisfactory fishing. Fall fingerlings are more economical and more reliable than spring fingerlings for this purpose.

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① MINNOWS IN TROUT PONDS.
PROPAGATION OF THE SILVERY MINNOW (HYBOGNATHUS NUCHALIS) IN PONDS. RANEY.
VOL. 71 Transactions American Fisheries Society 1941
Spawn inponds without vegetation, not too large.

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AN ECOLOGICAL INVESTIGATION OF STREAM INSECTS IN ALGONQUIN PARK, ONTARIO

By
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University of Toronto)

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AN ECOLOGICAL INVESTIGATION OF STREAM INSECTS IN ALGONQUIN PARK, ONTARIO

ABSTRACT

The effect of several ecological factors on the qualitative and quantitative distribution of stream insects in Algonquin Park, Ontario, was determined from data obtained by use of the cage-trap method of sampling the emergence of insects from unit areas in streams, at regular daily intervals.

Incidents that induced significant alterations in the physical nature of the streams were accompanied by marked reductions in the total insect population and a change in the faunal composition of the affected areas. Such incidents included a severe freshet, cessation of flow and subsequent desiccation of the stream bed, and transformation of a shallow rocky riffle into a deep sedimented pool by construction of a beaver dam.

A correlation was found between the total number of species in rocky riffle areas at different distances from the source, and the average water temperatures. The linear distribution of species was delimited by the water temperatures obtaining in different sections of the stream and this was correlated with the thermal tolerance of the immature stages.

Within the limits set by temperature the distribution of species was affected by other factors including rate of flow and nature of the bottom, two factors which are closely interrelated and fundamentally inseparable. The diversity of the fauna decreased from rubble, through gravel, and muck, to sand as the variety of utilizable microhabitats decreased. The observed distribution on different types of bottom was related to habitat preference and associated morphological adaptations in the species.

The seasonal emergence periods of different species were segregated and the species emerged in the same sequence each year. The date of first emergence and the length of the emergence period of a species differed from year to year and were determined by annual variations in water temperature.

The diurnal emergence of species showed a similar segregation in general, in that any one species emerged at the same time each day while different species emerged at different times. The maximum total emergence from a rapids during mid-summer occurred throughout the evening hours and the most important causal factor involved seemed to be a reduction in light intensity.

It has been suggested that the number of individuals present in any area depends primarily on the utilizable surface area of bottom particles exposed to the water.

INTRODUCTION

Although the importance of aquatic insects in the economy of running waters has long been recognized it has not been until recent years that any intensive work has been done to determine the intimate relationship that exists between the various environmental factors obtaining in streams and the abundance, variety, and distribution of the associated insect fauna. A complete understanding of this relationship is essential for a full appreciation of the complexus of stream populations and a prime requisite for the successful application of any stream improvement policy.

Of the recent publications pertaining to the ecology of stream insects many have treated the biological data purely qualitatively, others quantitatively; few contain analyses of the data from both these viewpoints. There is a scarcity of literature on studies of the invertebrate fauna of streams in which observations have been made at frequent, regular intervals. Although it is not always practicable to carry out such detailed investigations, when these are performed the data obtained are of considerable value in allowing other workers to place the proper interpretation on the results of more casual surveys.

Further, in almost all the stream investigations to date the information has been obtained by sampling the population of bottom fauna. Various methods were used such as the hand-dip method of Ludwig (1922), the Needham square-foot trap (Needham, P. R., 1928), the Peterson trap (Peterson, 1911) and Ekman dredge (Ekman, 1911) used by Gersbacher (1937), the United States Bureau of Fisheries one-foot trap described by Surber (1936), the basket method of Wene and Wickliff (1940), and the circular square-foot sampler devised by Hess (1941), which has been found particularly useful in gravel and rubble areas.

The cage-trap method, which samples the insect emergence from unit areas in streams, was introduced by Ide in 1937 (Ide, 1940). This method was found to be readily adaptable to a wide variety of stream conditions and allowed the investigator to determine the turnover of bottom fauna, rather than merely the population, both qualitatively and quantitatively, at frequent regular intervals. Ide found that his method gave a much higher value for the quantity of bottom fauna present in an area than was obtained by means of bottom sampling.

Ide's method was used in the present investigation which was carried out during the summer months of 1938 to 1941, inclusive, on a section of the Madawaska river system in Algonquin Park, Ontario. Detailed ecological information was obtained on the hourly, daily, seasonal, and annual variations of insect emergence; the effect of an intermittent flow and subsequent desiccation on the insect population of a rapids; the influence of a sudden freshet and concomitant molar action on aquatic insects; the effect of a reduction in the rate of flow and accompanying sedimentation on the insect fauna of a rapids; the role played by temperature in limiting the distribution of species in rocky, riffle areas at various distances from the source; and the distribution of species on different types of bottom in a restricted section of a stream.

HISTORICAL REVIEW

The effect of an intermittent flow and stagnation on the distribution and survival of aquatic insects in a stream of the Panama Rain-Forest was studied by Allee and Torvik (1927), who concluded that pH and dissolved oxygen content of the water were likely the most important factors affecting the distribution. Stehr and Branson (1938) carried out an extensive ecological study of an intermittent stream in Ohio and found that the insect fauna was limited both in numbers and variety during periods of low water.

Many authors have reported marked reductions in bottom fauna following severe floods and freshets in various streams. Moffett (1936) determined the change in the bottom fauna of some Utah streams variously affected by erosion, and found that floods of eroding proportions definitely destroyed existing stream populations. In general, there was a rapid recovery following abatement of the flood. Stehr and Branson (1938) concluded that such areas were repopulated in several ways, including migration of both immature and adult forms, emergence of species from hibernation, and reproduction of species that succeed in holding their positions in the stream.

The role played by current in limiting the distribution of insects in streams has been investigated by many workers including Clemens (1917), Dodds and Hisaw (1924 a and b, 1925 a), Hubault (1927), Muttkowski (1929), and Hora (1930). These studies emphasize the adaptations to and utilization of the current by typical lotic inhabitants. Wu (1931) found that in general the Simuliidae (Diptera) had an "inherent current demand," as opposed to a requirement for a high concentration of oxygen, which limited their distribution. In his work on the function of the gills of mayfly nymphs from different habitats, Wingfield (1939) came to the same conclusion.

Temperature has been shown by several investigators to limit the distribution of stream insects. Dodds and Hisaw (1925 b) determined the altitude range and zonation of the species of Plecoptera, Ephemeroptera, and Trichoptera along the valley of South Boulder creek, Colorado. They found that temperature was the main climatic factor responsible for the observed zonation. Ide (1935) studied the effect of temperature on the distribution of Ephemeroptera in the Nottawasaga river system, Ontario, and determined that temperature sets limits to the distribution of these insects within which are other limits correlated with other environmental factors. Whitney (1939) investigated the thermal resistance of several species of Ephemeroptera from various habitats in a stream and found a direct correlation between the resistance of nymphs to high temperatures and the temperature obtaining in the respective habitats.

Investigations on the effect of type of bottom on the insect distribution in streams have been stimulated, in recent years, through the extensive research on stream improvement that has been carried out in North America. Valuable contributions in this field have been made by Needham, J. G. (1927), Needham, P. R. (1927, 1928, 1932, 1934), Carpenter (1927), Percival and Whitehead (1929, 1930), Pate (1931, 1932, 1933), Moore *et al.* (1934), Morofsky (1935), Tarzwell (1936, 1937), Surber (1936, 1938), Gersbacher (1937), Wene and Wickcliff (1940), Linduska (1942) and others. In general, the quantitative results of these investigations have shown a productivity gradient of bottom organisms related to the types of bottom, decreasing from plant beds and silt through rubble and gravel to sand and bedrock. The qualitative results have shown the existence of distinct habitat preference for specific types of bottom by the majority of stream insects.

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DESCRIPTION OF DRAINAGE AREA, STREAMS AND STATION SITES

Mud creek and its tributary waters are situated along the southeast boundary of Algonquin Provincial Park, Ontario, at 45 degrees 33 minutes north latitude and 78 degrees 15 minutes west longitude. The system extends for 8 miles in a general southerly direction from the headwaters at an altitude of 1,400 feet to its termination in Galeairy lake at an altitude of 1,281 feet, and drains an area of 6 square miles (Topographical Survey of Canada, 1934). Galeairy lake is drained by the Madawaska river which empties into the Ottawa river at the town of Arnprior.

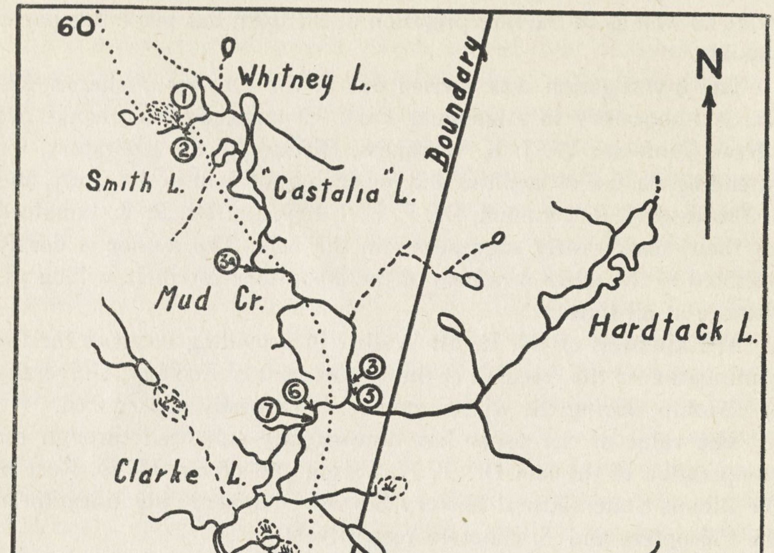

FIG. 1. Map of Mud creek drainage system. The numbers indicate the positions of the station sites used in the investigation.

The district in which Mud creek is located is part of the extensive pre-Cambrian shield area. The rock consists of masses of granitoid gneisses and light-coloured schists, characteristic formations of the Laurentian Period of the pre-Cambrian Era. This district is in the northern portion of the mixed conifer-hardwood forest. Prior to 1900 the area around Mud creek was heavily wooded with red and white pine, but at that time much of the original forest was cleared by intensive lumbering. In 1914 a devastating forest fire swept through this section and left it landmarked with charred rampikes which now jut characteristically here and there among the new growths of subclimax poplar and birch. On the exposed slopes, where the soil cover was thin, the fire burned through, baring extensive areas of rock, while the sheltered slopes and swamp sections were untouched and here considerable stands of conifers and hardwoods are still found.

The annual precipitation averages about 35 inches and this is evenly distributed throughout the seasons with the winter complement falling as snow. The average monthly mean temperatures range from 10 degrees Fahrenheit in January to 65 degrees in July.

Mud creek (figure 1) arises as the outlet of a small lake, 8 acres in area, which is surrounded by steep wooded hills. From its source the stream meanders 400 yards through an open beaver meadow and then widens into a small pond maintained by a beaver dam 8 feet high. The overflow and seepage water from the dam flow intermittently along a narrow rocky channel 3.5 feet wide with vertical banks 2 feet high. The banks support a dense growth of grasses and shrubs which shades the stream throughout most of the day. Station 1 (figure 2) was situated in this section of the stream, 50 yards below the beaver dam. This section of the stream dries up in midsummer in some years.

Station 2 was selected in a rocky riffle area 150 yards downstream from station 1 A small volume of cold water that flows continuously from a sheltered sphagnum bog and joins the stream 50 yards above station 2 provides a permanent flow. The flood channel at station 2 is 8 feet wide with sloping banks covered with grasses and shrubs but these are not dense enough to shade the stream completely during the afternoon period of each day. Extensive tufts of aquatic mosses, including *Fontinalis dalecarlica* Bry. Eur. and *Chiloscyphus fragilis* (Roth) Schiffn., trail in the current from the rocks at the water's edge. From station 2 the stream flows down a steep rocky decline and empties into Whitney lake.

Whitney lake has an area of 22 acres and a maximum depth of 30 feet. In addition to the small permanent stream described above, two intermittent streams that flow only during the spring and periods of heavy rain, empty into the lake. The water passes through a deep narrows into "Castalia" lake which is a shallow, elongate lake of 43 acres and has a maximum depth of 17 feet. One stream with a permanent flow empties into "Castalia" lake and the lake is also fed from Smith lake which has an area of 10 acres, a maximum depth of 25 feet, and one temporary stream flowing into it.

The water in all these lakes is distinctly brown and acid in reaction. There is a sharp thermocline at 15 feet during midsummer. The surrounding shores are characterized by wooded slopes alternating with low marshy areas which support dense growths of alder and various bog plants, while rooted aquatic plants are abundant in the shallow shore areas of the lakes.

From "Castalia" lake to Clarke lake Mud creek averages 10 feet in width and one foot in depth throughout most of the summer. There are frequent riffles where the stream flows rapidly over bedrock, rubble, or gravel, followed by short, deep pools with mucky bottoms. There are several beaver dams in this section which vary in size from mere obstructions to the main current to dams that flood an area as large as 4 acres. The stream is bordered with alder, birch, and poplar, with grasses and sedges at the water's edge. This vegetation protects the stream from direct insolation with the exception of the beaver ponds and wide parts of the stream. Four small streams join Mud creek in this section, three of which have a permanent flow. Stations 3a, 3, 5, 6, and 7 were selected in this part of the system.

Station 3a (figure 4) was situated 800 yards downstream from "Castalia" lake in the centre of a rocky riffle. The flood channel at the station was 8 feet wide with vertical banks which were covered with herbs and bushes. A few sedges occurred at the stream margin. The stream continued along a narrow rocky channel for about one mile and thence emerged into a large open meadow, through which it meandered in a deep, silted channel. The water flowed over a falls 7 feet high at the end of the meadow and passed down a short rocky rapids in which station 3 was established. The flood channel in this part of the stream was 18 feet wide. Station 5 was situated 20 feet downstream from station 3 in a deep placid pool in which the bot-

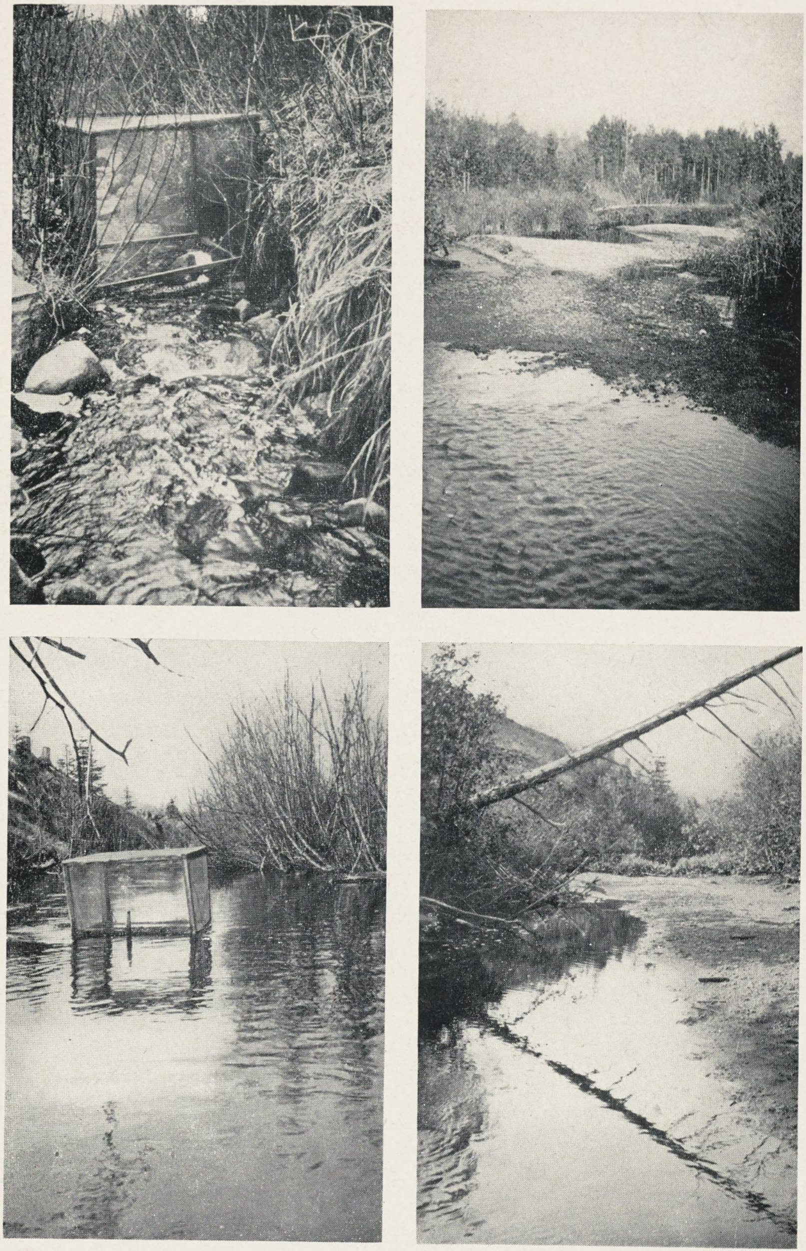

FIG. 2.—Illustrations of stations in the stream.

Upper left —Station 1, spring 1940.
Upper right—View of gravel bar below Station 6, summer 1940.
Lower left —Station 7, spring 1940.
Lower right—View of sand bar below Station 7, summer 1940.

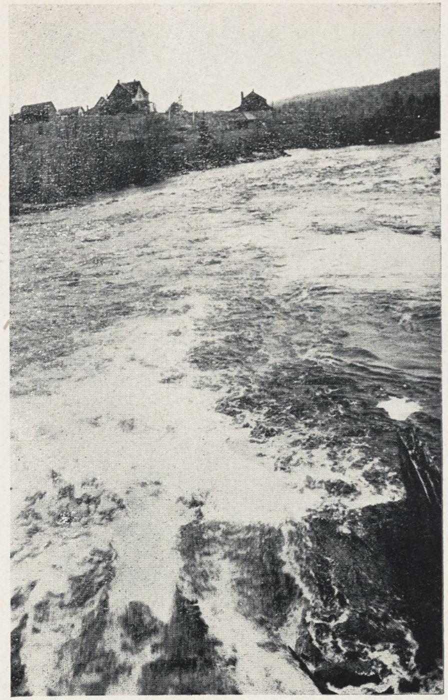

Fig. 3.—The Madawaska river, spring 1940, looking northeast from the dam at Whitney, Ontario. Stations 4, 4A and 4B were established in the right foreground.

Fig. 4.—A cage-trap in position in the stream. Station 3a, May 10, 1940.

tom consisted of muck and decaying organic matter. Clumps of the sedge, *Carex rostrata* Stokes, were present in the stream but there were no clumps in the station site proper. From station 5 the stream flowed through a dense alder swamp for 400 yards and thence opened into a clearing and flowed down a long, shallow, gravel riffle in which station 6 was located. The flood channel was 16 feet wide and was full and flowing during the spring but the stream was reduced in the summer months and long gravel bars became exposed (figure 2). The banks were covered with herbs and grasses but these were too low to shade the stream during most of the day. Station 7 (figure 2) was located 200 feet below station 6 where the current was reduced and the bottom consisted of fine sand. The flood channel here was 14 feet wide and the banks were covered with grasses, herbs, and alders which effectively shaded this part of the stream. A wide sand bar was exposed here during the summer period of low water (figure 2).

Clarke lake has an area of 51 acres and a maximum depth of 38 feet. The water is dark brown, acid in reaction, and there is a sharp thermocline between 15 and 20 feet in the summer period. Three small permanent streams empty into the lake. From Clarke lake to Mud bay, Mud creek flows sluggishly through a thick alder swamp. The channel averages 4 feet in width and 3 feet in depth and the bottom consists of sand and gravel covered with silt and organic detritus. Mud creek empties into Mud bay through a wide marshy delta in which the stream is diverted into several channels.

Mud bay possesses a relatively narrow channel of open water which is bounded for 200 yards on either side by shallows with numerous stumps and deadheads rising above the water surface. The water level in Galeairy lake is maintained by a dam constructed across the Madawaska river at the town of Whitney. This has flooded Mud bay and Mud creek back as far as Clarke lake so that it seems probable that the stream originally flowed directly into Galeairy lake.

Stations 4, 4a, and 4b were located in the Madawaska river (figure 3) immediately below the dam in a large rocky rapids. The volume of flow through the sluices of the dam was so great that the stations had to be selected to one side of the main current. The flood channel of the river is 150 feet wide and is strewn with large boulders many of which measure 10 feet in diameter. Small stands of poplar and birch, alder clusters, grasses and shrubs cover the river banks, but because of the width of the channel the stations were exposed to direct sunlight throughout most of the day.

The Madawaska river is representative of the large river conditions found in Algonquin Park while Mud creek is representative of the smaller streams so numerous in this district.

Physico-Chemical Conditions

The station sites were selected to provide information on specific phases of the ecology of stream insects. Stations, 1, 2, 3a, and 4 were chosen in the centres of rocky riffles, throughout the length of the river system, in order to minimize the effect of factors other than distance from the source on the insect distribution. In a like manner, stations 5, 6, and 7 were selected in a short section of Mud creek,

Table 1.—Average physical and chemical conditions at the stations in the summer of 1938. The figures represent the average of six determinations made on June 17, July 16 and 30, August 11 and 26, and September 9, with the exception of those for the oxygen content, percentage saturation and hydrogen ion concentration at stations 5, 6, and 7 where a single water analysis was made on August 12.

	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6	Station 7
Type of bottom....	Rubble	Rubble	Rubble	Rubble	Muck	Gravel	Sand
Width in feet	1.3	5.8	12.8	85.0	12.5	8.7	9.7
Depth in inches	1.6	3.3	5.7	21.5	14.9	6.7	12.6
Rate of flow in feet/sec.	0.1	0.4	0.9	2.3	0.1	0.8	0.3
Volume of flow in cu. ft/sec..	0.1	0.5	4.8	288.0	1.9	4.0	3.2
Colour.....	69	56	115	32	...	...	...
Dissolved oxygen in cc/l......	6.7	7.6	6.6	6.4	6.9	6.3	6.3
Percentage saturation.	91	97	93	99	91	92	92
Hydrogen ion concentration ...	6.1	6.2	6.6	6.4	6.7	6.5	6.5

close to station 3, where different types of bottom prevailed so that the effect of factors other than type of bottom would be minimized. Sations 4a and 4b were established beside station 4 in an extensive rapids where all conditions were apparently identical.

Observations of certain physical and chemical properties of the water, including rate and volume of flow, colour, oxygen content, and pH, were made only at intervals throughout the investigation, while the depth of water at station 3 and the water temperature at each station were recorded daily.

To illustrate representative water conditions at the stations, table 1 has been prepared from determinations made during the summer of 1938. The values in the table are the averages of six observations made on June 17, July 16 and 30, August 11 and 26, and September 9, with the exception of the pH, oxygen content and percentage saturation at stations 5, 6, and 7 for which the values represent the results of a single water analysis made on August 12. Station 3a, 4a, and 4b are not included in the table since these were not in operation in 1938. However, from observations made in later years, it was found that the conditions at station 3a approximated those at station 3, and at stations 4a and 4b were identical with station 4.

Apparatus and Methods

The water temperature was recorded continuously at station 3 by means of a Negretti and Zambra distance recording thermometer which was in operation in each of the three years. The temperatures at all other stations were obtained from maximum-minimum or hand thermometers. Daily readings were made at the times the stations were visited. All times referred to are Eastern Daylight Saving Time.

The depth of water was recorded daily at station 3. This was determined from a stake graduated in inches which was driven into the stream bed with a zero mark at the surface of the bottom particles. Occasional records of depth were made at all other stations by determining the average of several direct measurements made with a yardstick.

The rate of flow of water was obtained in 1938 by submerging a paddle, attached to a spring, to a standard depth and reading the value from a graduated scale along which the paddle was deflected by the current (Solman, 1939). This apparatus was calibrated so that the readings could be converted into rate of flow in feet per second. In the succeeding years the rate was determined by recording the average time required for a small piece of wood to traverse a measured distance in the stream.

The volume of flow was calculated from the equation of Embody (1927) which contains a factor for correction of "bottom drag."

The colour of the water was determined by comparison with a series of coloured glass plates which had been calibrated against a set of platinum cobalt standards (U.S. Geological Survey, 1902).

Table 2.—Periods during which collections were made at the stations in 1938, 1939, 1940, and 1941.

Station number	1938	1939	1940	1941
1	May 31 - Sept. 18	May 17 - Sept. 11	......	......
2	May 25 - Sept. 18	May 17 - Sept. 11	May 11 - June 30	May 8 - June 30
3	May 25 - Sept. 18	May 17 - Sept. 11	May 12 - Aug. 31	......
3a	......	......	May 11 - Aug. 31	May 8 - June 30
4	June 6 - Sept. 18	May 17 - Sept. 11	May 25 - July 22	......
4A	......	......	......	July 3 - July 13
4B	......	......	......	July 3 - July 13
5	June 29 - Sept. 17	June 6 - Sept. 11	June 1 - Aug. 31	......
6	June 29 - Sept. 17	June 6 - Sept. 11	May 12 - Aug. 31	......
7	June 29 - Sept. 17	June 6 - Sept. 11	May 11 - Aug. 31	......

The dissolved oxygen was determined by Miller's method as described by De Laporte (1920). The percentage saturation of the water was obtained from Roscoe and Lundt's table; no correction was made for variations in atmospheric pressure.

The pH was determined by means of a Lamotte optical comparator (Lamotte Co., Baltimore, Md.).

Oxygen

The water at all the stations was well oxygenated throughout the summer season with a general increase in the dissolved oxygen content occurring during the latter part of August and into September. In 1938 the values ranged from 5.6 cc/1 at station 1 on June 17, to 9.8 cc/1 at station 2 on September 9. The dissolved oxygen content of the water at station 2 was consistently higher than that at the other stations and probably resulted from the photosynthetic activity of aquatic mosses which covered the rocks at the station site.

The percentage saturation in 1938 ranged from 84 at station 3 on July 16, to 112 at station 2 on September 9; the average summer value at each station approximated complete saturation.

Hydrogen Ion Concentration

The water at all the stations was acid in reaction with a range of 6.1 to 6.7 recorded during the summer months of 1938.

Type of Bottom

The bottom at stations 1, 2, 3a, 4, 4a, and 4b consisted of rubble and rocks overlying coarse gravel. Station 3 was characterized by this same type of bottom during 1938 and up to the end of June in 1939. However, at this date beavers constructed a dam across the stream, 100 yards below the station, which reduced the rate of flow and altered the nature of the bottom since sand, silt, and organic detritus were deposited among the rubble as the transporting power of the stream was reduced. This condition persisted throughout the remaining years of the investigation.

A thick layer of soft muck constituted the bottom at station 5 and was made up of fine inorganic particles along with a considerable amount of decaying plant remains. Station 6 was selected on a gravel bottom with the individual pebbles averaging about ¾ of an inch in greatest diameter. The bottom at station 7 consisted of fine sand of which 10.9, 72.6, 15.9, and 0.6 per cent was retained in number 10, 40, 80, and 200 standard sieves, respectively.

Flow

A permanent flow of water was maintained at all the stations during the four summers of the investigation with the exception of station 1 where an intermittent flow occurred in the midsummer of 1938.

The rate and volume of flow at the riffle stations increased downstream from the source region, represented by stations 1 and 2, to the lower, large river region of the system which was represented by station 4. The rate and volume of flow at stations, 5, 6, and 7 were directly related to the types of bottom existing at the respective sites. The lowest values at all seasons were recorded at station 5 and increased through station 7 to station 6.

Maximum conditions of flow prevailed at all the stations during the spring flood period in May of each year. After the flood the flow gradually decreased and minimum values generally were recorded in late July and early August, although this depended largely on the weather. Severe thunderstorms or prolonged periods of steady rain induced secondary maxima of short duration which simulated the spring flood in the small source streams.

Depth

In general the average depth of water at the stations increased as the distance from the source region increased. The lowest value was recorded at station 1 and the depth increased through stations 2, 3a, 3, and 4 under normal conditions. The depth at stations 5, 6, and 7, which were characterized by different types of bottom, decreased from station 5 through station 7 to station 6 as the size of the bottom particles increased.

A typical record of the seasonal change is shown in figure 1, Sprules (1941). There is a rapid decrease during May as the spring run-off subsided, followed by a long period of steady decrease in the summer months during which time minor fluctuations occur, dependent on local rainfall. A slight increase in depth was observed in the early fall season which was probably related to the decreased rate of evaporation.

Colour

The water at all the stations was brown, a condition which exists in most waters of this region. The values obtained from water samples taken during the summer of 1938 ranged from 27 at station 4 on August 11, to 145 at station 3 on July 16. The average summer values for 1938 ranged from 32 at station 4 to 115 at station 3. The relatively high values found at station 3 probably resulted from an increased amount of dissolved material added to the water as it meandered through the open meadow above the site of the station.

Temperature

The water temperature at each station was determined once a day, in most cases, at the time the station was visited. Thus a direct comparison of the temperatures at the different stations could not be made, as there was an average time lapse of about 3 hours between the times at which the first and last stations were visited each day. In order to minimize the effect of this difference in times of observation, the average of all the temperature readings obtained from a station for a complete summer was determined, along with the average time at which these readings were made. The average summer temperature at station 3, for the same time of day, was determined from the charts of the constant recording thermometer which was in operation at this station throughout the four years of the investigation. The difference, in degrees Fahrenheit, between the average summer temperature at each station at a specific time of day and the average summer temperature at station 3 for the same time of day, was determined for each year. The average of these differences has been used to obtain an index of the temperature relationships of the stations.

The average summer water temperature at the rocky riffle stations which were selected at different distances from the source, increased downstream from station 2 through stations 3a and 3 to station 4. For the complete period of the investigation the average temperature at station 3 was 62.0 degrees Fahrenheit. The temperature at station 2 averaged 6.1 degrees lower than station 3, station 3a averaged 1.7 degrees lower than station 3 and station 4 averaged 5.4 degrees higher than station 3. Although station 1 was located close to station 2 in the upper section of the stream, the average temperature was only 1.3 degrees lower than that at station 3. The relatively high temperature prevailing at this station, when its position with respect to the source is considered, was dependent on the intermittent nature of the flow at the station.

The average temperature differences between stations 3, 5, 6, and 7, which were selected close together in one section of Mud creek, were small. The temperature at stations 6 and 7 averaged 0.2 and 0.3 degrees Fahrenheit higher than station 3, while at station 5 the average temperature was 0.4 degrees lower than that at station 3.

The largest diurnal temperature fluctuations were recorded at station 3 during the latter part of July and early August each year and amounted to 17.5 degrees Fahrenheit in some instances. The diurnal fluctuations at station 2, which was situated close to the source, and at station 4 where there was a much larger volume of water, were smaller than at station 3. The maximum water temperature recorded during the investigation was 85.0 degrees Fahrenheit which occurred at station 3 on August 16, 1938. Although the average summer temperature at station 4 was greater than that at station 3, the maximum temperature found at the former station was only 79.5 degrees Fahrenheit.

The same seasonal trend of water temperature prevailed at all the stations and consisted of a rapid increase during May followed by a prolonged period of more or less constant high summer temperature and a rapid decrease in September. The temperature at station 2 was lower than at station 3 at all seasons although a much greater deviation occurred in the summer months than in the spring or fall. The average temperature at station 4 was, in general, higher than that at station 3 but during May each year the converse relationship existed resulting from the greater volume of water to be heated at the former station.

In order to obtain an index of the annual temperature variation in the stream, the accumulated temperature above 32.0 degrees Fahrenheit was determined for station 3 from June 1 to September 13 each year by summing the average of the daily maximum and minimum temperatures. Although the total accumulated heat varied significantly from year to year when the values at some particular date during the summers were compared, it was found that the total accumulated heat acquired by the stream over a long period showed little annual variation. Values of 3,470, 3,450, 3,240 and 3,470 day-degrees were obtained in 1938, 1939, 1940, and 1941, respectively. It is probable that the small annual differences observed would be reduced if the early spring and late fall temperatures, from ice break-up to freeze-up, were included in the compilation of these figures. Thus it would seem that the total heat budget in any specific section of a stream shows little annual variation although the seasonal disposition of the heat may vary considerably from year to year depending on annual climatic differences.

Biological Conditions

Apparatus and Methods

The cage-traps (figure 4) used in this investigation were introduced by Ide in 1937 (Ide, 1940), and have been used by him in similar stream studies since that time.

In general, collections were made daily but during the summer of 1938 the cages at stations 5, 6, and 7 were left in position in the stream but were visited on only two consecutive days each week. In this latter case the cages were cleared the first day and a collection made the second day which thus represented the insect emergence for the preceding twenty-four hour interval. Further modifications of the general method were used at stations 4, 4a, and 4b, where occasional diurnal series of collections were made in 1939, 1940, and 1941. These collections were made at one-, two- or four-hour intervals for a twenty-four-hour period.

In the examination of the collections the Plecoptera, Ephemeroptera, and Trichoptera were identified with species whenever possible. These orders were selected for specific determination since they constituted by far the greatest volume of material in the collections. The remaining aquatic insects collected were identified with family only. In the ensuing discussions of the quantitative distribution, the total insect emergence has been considered under six separate headings, the Plecoptera, Ephemeroptera, Trichoptera, Chironomidae (Diptera), Simuliidae (Diptera), and "Miscellaneous." The last heading is composed of a heterogeneous assemblage of insects which occurred in relatively small numbers in the collections and includes Empidae (Diptera), Ceratopogonidae (Diptera), Tipulidae (Diptera), Hemerobiidae (Neuroptera), and Coenagrionidae (Odonata) for the most part.

Sources of Error

There are several sources of error associated with the cage-trap method of collecting aquatic insects. Many of these have been pointed out by Ide (1940). These, briefly, are the introduction of biting insects on the person of the collector, the drifting in of occasional terrestrial forms, passage of small species through the mesh of the cage, reduction in numbers after emergence by the predation of spiders and Empidae, occasional escapes when the cage door is open, shading of the enclosed area, and possible destruction of the aquatic stages through disturbance of bottom when the collector moves about.

Precautions were taken to reduce those errors as much as possible. The population of biting insects was taken as double the number of males, which do not bite and thus are not likely to have entered on the collector. Terrestrial insects were disregarded. The cage was tapped to free the door of insects before it was opened. A seat was constructed in one corner of the cage to reduce the necessity of disturbing the bottom.

Certain observations were made during the current investigation which supplement the previous findings. Ide's estimate of 200 as the probable maximum number of Simuliidae to be carried into a cage during a season appears to be low for some situations. A new estimate of the number of insects to enter a cage in this way was obtained from analyses of the collections made at station 5 in 1939 and 1940. This station was characterized by deep, quiet water and a mucky bottom while the larvae and pupae of Simuliidae are found in general in shallow, swiftly-flowing sections of a stream with a rocky bottom. No male individuals were found in the collections while a total of 548 and 826 females were collected in 1939 and 1940, respectively, the majority in both years occurring in the month of June. Under the circumstances it may be taken that virtually all these individuals were carried into the cage by the collector.

The modification of the method of taking daily collections used in 1938 (page 30) created an error in the total number of insects collected at station 6 in that year. A total of 1,942 insects were collected of which 1,753 were Chironomidae (Diptera). These numbers are in error since for a short period in midsummer the number of Chironomidae present the day the cage was cleared each week was so great that these could not all be removed in the time available to complete the collection. Thus, although the collector concentrated on the removal of the representatives of the other insect groups and succeeded in removing all these, a certain number of Chironomidae were left and these augmented the number of insects collected the following day. This particular instance was the only one in which such a discrepancy arose since at all other stations the clearance from the cages was complete each day.

A previously unrecognized error which results from the practice of collecting from the cages only once each day was brought to light from the results of a diurnal series of collections made at the site of station 4. This error is perhaps the most significant of all. In 1939, two series were run at two-hour intervals, the first from 11.00 a.m. August 4 to 11.00 a.m. August 5 and the second during the same hours on August 14 and 15. In 1940, a similar series was run on July 4 and 5. The results of these collections showed that the number of insects collected over a twenty-four-hour period during which

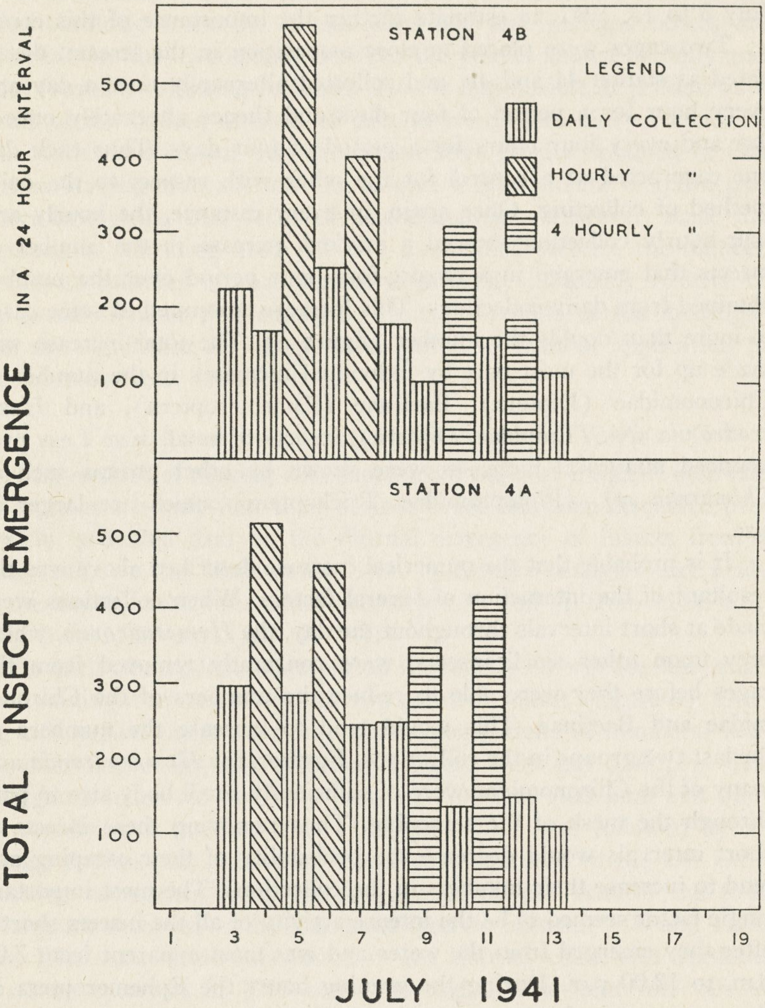

FIG. 5. The total insect emergence for twenty-four-hour periods at stations 4a and 4b from July 3rd to 13th inclusive, 1941, showing the results of collecting the cages once a day, every hour and at four-hour intervals.

collections were made at two-hour intervals was more than double the number obtained when only one collection was made in twenty-four hours.

A somewhat more elaborate experiment was carried out from July 3 to 13, 1941, to estimate further the importance of this error. Two cages were placed in close association in the stream, designated as station 4a and 4b, and collected alternately once a day and every hour for a period of four days and thence alternately once a day and every four hours for a period of four days. Thus each day one cage acted as a control for the other with respect to the daily method of collecting. Once again, in every instance, the hourly and four-hourly collection showed a marked increase in the number of insects that emerged in a twenty-four-hour period over the number obtained from daily collections. This increase amounted in some cases to more than double the number (figure 5). The total increase was made up for the most part by individual increases in the number of Chironomidae (Diptera), Baetinae (Ephemeroptera), and *Hemerodromia spp.* (Empidae, Diptera), insects of small size. Less pronounced numerical increases were shown by other groups such as *Chimarrha spp.* (Philoptomidae, Trichoptera) which are larger in size.

It is probable that the numerical increase described above was the resultant of the interaction of several factors. When collections were made at short intervals throughout the day, the *Hemerodromia,* which prey upon other small insects, were constantly removed from the cages before they were able to reduce the numbers of the Chironomidae and Baetinae. This would tend to increase the numbers of the last two groups in the collections. Further, the *Hemerodromia* and many of the Chironomidae were of sufficiently small body size to pass through the mesh of the screening. Thus removing these insects at short intervals would decrease the probability of their escaping and tend to increase their numbers in the collections. The most important single factor seemed to be the intense activity of all the insects shortly after they emerged from the water and was most apparent from 7.00 p.m. to 12.00 p.m. During the evening hours the Ephemeroptera in the cages were almost constantly on the wing and these were followed later by the Chironomidae and Trichoptera, which showed the same phenomenon. This activity caused many insects to fall to the water surface and be carried out of the cages by the current. Collecting at short intervals reduced this possibility and tended to increase the numbers of all the groups in the collections.

It is desirable that a correction factor be established to meet the error resulting from the causes discussed and perhaps others responsible for the discrepancy between the results shown by daily and more frequent collecting methods. This is imposssible at present as a result of the limited amount of data at hand. The diurnal series of collections have shown that the quantitative results obtained in this stream investigation are too low to give a true picture of the actual insect emergence that occurred at the stations. However, since the methods of collecting used fall into a standard pattern, the number of insects collected at each station is probably uniformly relative to the actual number that emerged. Thus the results of the investigation are significant for comparative purposes without application of a correction factor for this error.

The Diurnal Emergence of Insects from a Rapids

The method of making collections from cages at frequent intervals throughout a twenty-four-hour period, which has been discussed previously, provided data on the diurnal emergence of insects from a rocky riffle in the Madawaska river. A detailed analysis was made of the hourly collections taken at stations 4a and 4b from 11.00 a.m. July 3 to 11.00 a.m. July 7, 1941.

In each twenty-four-hour period the hourly emergence was small from midnight up to an hour or two prior to sunset (figure 6). During this period there were only minor fluctuations in numbers, with the minimum emergence occurring between 3.00 and 6.00 p.m. The emergence increased suddenly between 7.00 and 9.00 p.m. and built up rapidly to a maximum at 11.00 p.m. This was followed by an abrupt decrease at 12.00 p.m. and thence returned to the low early morning emergence level. An average of 60 per cent of the total emergence occurred in the four-hour interval between 8.00 and 12.00 p.m. The same cycle was found in the diurnal collections made at two-hour intervals in 1939 and 1940 and at four-hour intervals in 1941.

The separate insect groups showed differences in the time of maximum emergence during a twenty-four-hour period. The Ephemeroptera emerged, for the most part, between 7.00 and 10.00 p.m., although occasional individuals were obtained in the collections made during the late morning hours and early afternoon. The maximum emergence of Trichoptera and Chironomidae occurred between 10.00 and 11.00 p.m., and the coincidence of the separate maxima of these two groups was responsible for the 11.00 p.m. maximum observed when the total quantitative emergence of insects was considered. Both these groups continued to emerge in reduced numbers throughout the day and night. The Simuliidae emerged throughout the daylight hours and in general were absent from the collections made during darkness. The Empidae ("Miscellaneous") emerged in small numbers during the early afternoon, reached a maximum between 7.00 and 9.00 p.m., and did not emerge during the night. A single species of Plecoptera was obtained during this study and it emerged from 9.00 p.m. to 1.00 a.m. with its maximum emergence at 11.00 p.m.

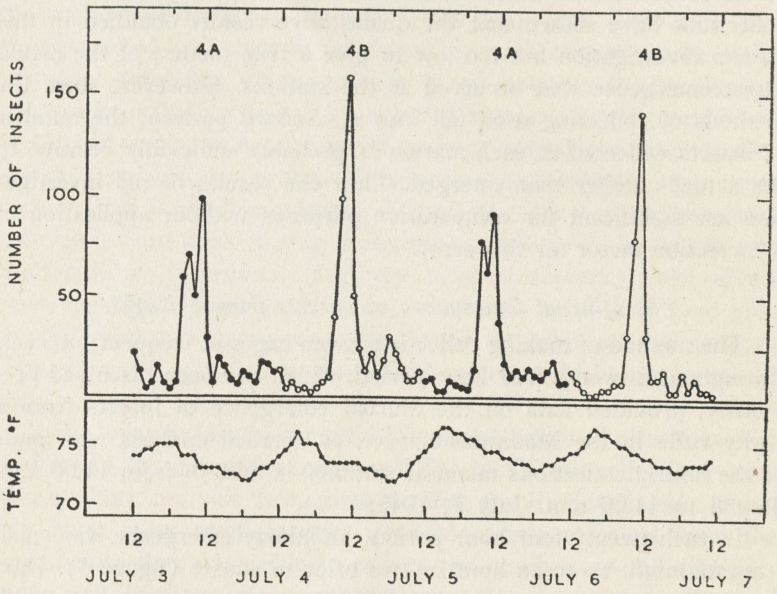

FIG. 6. The total hourly emergence of insects and water temperature in degrees Faharenheit at stations 4a and 4b from July 3rd to July 7th, 1941, beginning at noon.

More detailed analyses of the hourly collections disclosed that the species within any one group of insects emerged at specific times each day. For example, of the Ephemeroptera obtained during the investigation at stations 4a and 4b, *Pseudocloeon virile* was taken only in the 4.00 and 5.00 p.m. collections; *Ephemerella sp.* emerged between 7.00 and 8.00 p.m.; *Baetis sp.* (near *pygmaeus*) between 7.00 and 9.00 p.m. with the maximum in every instance between 8.00 and 9.00 p.m.; *Baetis flavistriga, Leptophlebia volitans, Stenonema rubrum,* and *Stenonema luteum* showed their maximum emergence between 9.00 and 10.00 p.m.; and *Stenonema heterotarsale* emerged between 10.00 and 11.00 p.m. The relation of the times of emergence of these species was observed each day at both stations. One exception was found in that *Isonychia bicolor* emerged between 7.00 and 9.00 p.m. in general, but on July 4 at station 4a this species emerged between 7.00 and 9.00 a.m.

The maxima of temperature and insect emergence did not coincide in any twenty-four-hour period. The maximum temperature occurred, in general, between 3.00 and 5.00 p.m. and the minimum at about 6.00 a.m., while the maximum emergence occurred at 11.00 p.m. The emergence began to build up to this maximum between 8.00 and 9.00 p.m. which corresponds with the onset of sundown and indicates that the final impetus for emergence is related to a decrease in light intensity. It is probable that temperature is of importance in completing the development of an insect on a specific date but emergence does not occur until the following period of decreased light intensity which seems to stimulate activity and result in the completion of the aquatic sojourn of the insect.

Other investigators have obtained similar results regarding the time of emergence of aquatic insects. Miller (1941) found that the emergence of Chironomidae from shallow water in Costello lake, Algonquin Park, occurred between 4.00 and 7.00 a.m. (Standard Time); in the deep water the emergence was equal throughout the day. Scott and Opdyke (1941) investigated the emergence of insects from Winona lake, Indiana, and found that the Diptera emerged, for the most part, between 6.00 and 12.00 p.m., with in one case a smaller mode from 4.00 to 6.00 a.m. (Standard Time). They state that the Trichoptera emerged during the first part of the night, in general, but that a few emerged during the day.

The results of the present investigation showed conclusively that the diurnal insect emergence reached a maximum between 10.00 and 11.00 p.m. in a typical rapids in the Madawaska River. It cannot be assumed, however, that this relationship holds for other streams nor for other seasons in the same stream. Since different species emerge at different times of day, the specific composition of the bulk of emerging insects would affect the time of maximum emergence in any specific section of a stream.

The Effect of a Freshet on the Insect Fauna of a Stream

During a study of the distribution of insects on different types of bottom, a condition arose which afforded an opportunity of determining the effect of a sudden freshet on the insect fauna of a stream. A beaver dam, situated at the outlet of "Castalia" lake, broke suddenly on May 25, 1940, as the result of increased pressure brought to bear by the rise in lake level following an extended period of heavy rainfall. The water level in the lake dropped 3 feet during the day and this enormous volume of water cascaded down Mud creek, overflowing the banks and causing considerable damage in that area. This condition of flood prevailed for 7 days as the water subsided gradually and the stream finally returned to a normal flow. During this period large rocks were observed rolling slowly downstream and gravel and sand sections were moved as a whole and deposited in new areas.

Since the freshet occurred in the early spring, the number of insects emerging each day prior to the flood was too small to determine its immediate effect on the population. Coupled with this was the fact that the cages could not be maintained in the stream during the height of the flood. However, the result of the flood was determined by comparing the insect emergence at stations 5, 6, and 7 for the period June 6 to August 31 in 1939, which may be considered a normal season, and in 1940 (table 3).

The total insect emergence for this period at station 5 corresponded closely in the two years, with 1,932 and 1,827 individuals emerging in 1939 and 1940 respectively, a decrease of 5.6 per cent in the latter year. This decrease probably represents, for the most part, annual variation in the insect emergence, since the station was situated in a deep, slow-flowing pool, to one side of the main current, where the effect of the freshet would be minimized.

Table 3.—Number of insects that emerged at stations 5, 6, and 7 from June 6 to August 31, 1939 and 1940.

	Station 5		Station 6		Station 7	
	1939	1940	1939	1940	1939	1940
Plecoptera......	0	1	105	10	7	5
Ephemeroptera..	608	138	191	64	385	28
Trichoptera.....	56	110	34	36	15	20
Chironomidae...	1,247	1,575	1,187	595	1,360	757
Simuliidae......	0	0	590	562	10	18
"Miscellaneous".	21	3	88	29	34	44
Total......	1,932	1,827	2,195	1,296	1,811	872

Stations 6 and 7 were located in the centre of the stream in a relatively shallow section where the physical effect of the freshet would be maximal. A total of 2,195 and 1,296 insects emerged at station 6 in 1939 and 1940 respectively, a decrease of 41.0 per cent in the latter year. At station 7 a total of 1,811 and 872 insects emerged in 1939 and 1940 respectively, a decrease of 51.9 per cent in the summer following the freshet. Thus when these percentage decreases are compared with the 5.6 per cent decrease noted at station 5, which represents the probable annual variation in numbers, it is apparent that the freshet brought about a significant decrease in the summer populations at stations 6 and 7.

The total numerical decrease observed at stations 6 and 7 in 1940 resulted from the individual decreases in the numbers of Plecoptera, Ephemeroptera, and Chironomidae, for the most part, while only small differences were found in the numbers of Trichoptera and Simuliidae that emerged each year. The "Miscellaneous" group is too heterogeneous to be discussed satisfactorily. These results indicate that the forms with free-roving immature stages were reduced numerically while those with attached larvae and pupae were not affected appreciably by the freshet.

The role played by freshets in decreasing the population of a stream has been reported by several investigators, including Needham (1927), Tarzwell (1937), Surber (1938), Stehr (1938), and others. In general it has been found that during periods of high water in streams many of the bottom organisms are forced from their ecological niche, carried downstream and deposited in slow-flowing pools. If the gradient in the stream is gradual the freshet may detach only the insects that are free-roving on the surface of the bottom particles, but if the gradient is steep even those forms that adhere tightly to the particles will be moved and thus dislodge or crush the insects present. Stehr (1938) reports that serious floods may carry much of the invertebrate fauna away while the population is restored by minor floods washing individuals into the area and by migration back to the area. Needham (1927) placed a drift net across a stream during a spring flood and found that almost every kind of aquatic organism found in the stream was washed into the net. The majority of these were injured by the grinding action of the bottom particles and even larvae of Simuliidae, which normally live in fixed positions in swift water, were found in the net. Tarzwell (1937) found that a severe spring flood in streams of the Tonto Forest in Arizona reduced the amount of "bottom food" by almost half. This figure is in close agreement with the 41.0 and 51.9 per cent reductions in emergence obtained in the present study.

The results of this investigation showed that the number of insects that emerged from a scoured section of a stream, following a severe freshet, was considerably lower than would be expected under more normal conditions. It is probable that the number that do emerge from such an area is made up of insects that were able to withstand the increased flow and maintain their original positions in the stream or find suitable shelter, insects that were deposited in the area as the freshet subsided and were able to establish themselves in the new habitat, and insects that migrated into the area to obtain more suitable environmental conditions.

The effect of freshets on insect populations is profound in shallow sections of streams and areas with unstable bottoms, while the effect is greatly reduced in deep sections and areas with relatively stable bottoms. One exception to this generalization is obvious since smooth bedrock, although the most stable type of bottom found in streams, offers no protection during a freshet and the meagre insect fauna associated with this type of bottom would be quickly washed away.

Within any particular habitat, the resistance of the existing species to freshets is related to their mode of life. The free-roving species are readily dislodged unless able to acquire protection in the lee of bottom particles or in crevices, while the species with attached larvae or pupae and burrowing forms are able to withstand a much greater current. However, these species are just as vulnerable as the free-roving types to the destruction wrought by molar action which accompanies severe freshets in areas where the bottom is unstable.

The Effect of Intermittent Flow on the Insect Fauna of a Rapids

Many of the smaller streams of the Algonquin Park area are characterized by an intermittent flow and depend on run-off water and overflow from ponds for their volume. These streams assume considerable proportions during the spring flood and in periods of heavy local rainfall, but are reduced in size and in many cases dry up completely as the summer drought period sets in. A small flow is restored to these streams in the late summer and fall seasons.

Station 1 was situated in such a stream and here the volume of flow was dependent on the volume of water maintained in a beaver pond above. The stream dried up completely for periods during the summer of 1938 but was not completely dry at any time in 1939. An investigation of the insect fauna at the station was carried out to determine to what extent an intermittent flow and desiccation affected the insect population.

Quantitative Results

The insect emergence, when compared in 1938 and 1939 showed marked differences, and these were directly related to the relative drying of the stream bed in the two years. A total of 5,017 insects emerged from June 1 to September 11 in 1938, of which 4,003 or 79.8 per cent of the total emerged prior to July 17, at which date the stream bed at the station became dry, while 1,014 or 20.2 per cent emerged after July 17. The total emergence for the same period in 1939 was 4,899 individuals, which shows that annual variation in the total emergence was slight. However, the seasonal distribution of the insect emergence differed significantly in the two years, since 3,272 or 66.8 per cent emerged prior to July 17, while 1,627 or 33.2 per cent emerged after this date. In both years the majority of insects emerged in the period June 1 to July 17, but a greater proportion of the total emerged after July 17 in 1939 than in 1938. This relationship between seasonal emergence and continuity of flow was the result of definite changes in the different insect groups which were even more directly correlated with the nature of the flow.

All the Plecoptera, Ephemeroptera, Trichoptera[1] and Simuliidae that emerged in 1938 (table 4) were collected prior to July 17 while in 1939, 32.1 per cent of the total number of Plecoptera, 35.2 per cent of the Ephemeroptera, and 9.0 per cent of the Trichoptera emerged after July 17. In 1939, as was the case in 1938, there were no Simuliidae collected at the station after July 17, but since this group completed its emergence early in June each year, it is impossible from the results of this study to determine whether or not the drying up of a stream would affect its emergence. It seems probable from a consideration of the preferred habitat of the Simuliidae that this group should be included with the Plecoptera, Ephemeroptera, and Trichoptera as representative of groups unable to withstand desiccation, at least in their active aquatic stages.

The remaining two groups, Chironomidae and "Miscellaneous," were made up of individuals which were able to survive the desiccation, at least to some degree, since considerable numbers were collected after the stream became dry in 1938. Twenty per cent of the total emergence of Chironomidae in 1938 occurred during the period July 17 to September 11, and 34.7 per cent emerged in the same period in 1939. Part of this difference may be a result of annual variation in the seasonal emergence but it seems probable that, for the most part, it represents a reduction in the population occasioned by the desiccation in 1938.

Of the total number of "Miscellaneous" collected in 1938, 55.9 per cent were obtained in the period July 17 to September 11, while only 13.3 per cent were obtained in the same period in 1939. This apparent lack of correlation between the reduction in number of insects and intermittent flow resulted since the individuals in this group were not identified beyond family, and likely many individuals entered the cage from outside by crawling along the stream bed during the dry period and were, therefore, not truly aquatic. Stehr (1938) reported a rapid influx of terrestrial insects on to a stream bed once

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[1] Female individuals were collected while the stream was dry and probably gained entrance to the cage from outside.

TABLE 4.—Analysis of the total insect emergence at station 1 from June 1 to September 11 in 1938 and 1939.

Period	Plecoptera		Ephemeroptera		Trichoptera		Simuliidae		Chironomidae		"Miscellaneous"	
	1938	1939	1938	1939	1938	1939	1938	1939	1938	1939	1938	1939
June 1-30....	14	31	18	62	8	112	126	2	2,216	2,211	45	120
July 1-17....	0	5	41	304	4	11	0	0	1,512	377	19	37
July 17-31....	0	0	0	97	*1	0	0	0	373	71	37	14
Aug. 1-31....	0	17	0	88	*1	11	0	0	522	1,064	40	9
Sept. 1-11....	0	0	0	14	0	1	0	0	36	240	4	1

*Collected while the stream bed was dry. Probably gained entrance from outside.

it became dry, and this corroborates the above supposition since such forms would be included in the collections from the cage and those families which had aquatic counterparts would be included in the quantitative totals.

Qualitative Results

There were seven species of Plecoptera found at station 1 including *Nemoura venosa, Nemoura serrata, Leuctra duplicata, Alloperla mediana, Isoperla montana, Nemoura punctipennis,* and *Leuctra decepta.* The first six species were early summer forms which completed their emergence before July 17, and thus did not show the effect of an intermittent flow. *Leuctra decepta,* on the other hand, which emerges during the late summer, was not found at the station in 1938 but was present in 1939 (figure 7), indicating that it was eliminated in the former years as a result of the drying-up of the stream.

There were six species of Ephemeroptera found at the station. These fell into two main categories, one represented by *Baetis brunneicolor* (figure 7) and *Centroptilum convexum* which completed their emergence in the early summer and thus were not subjected to the drying in 1938, and the second by *Leptophlebia debilis* (figure 7), *Baetis sp.* (near *pygmaeus*), *Heptagenia pulla,* and *Stenonema carolina,* species which emerged later in the summer and were eliminated at the station in 1938.

There were thirteen species of Trichoptera found at the station of which *Hydropsyche betteni, Diplectrona modesta, Psychomyia diversa, Lepidostoma sp., Limnephilus consocius, Dolophilus moestus, Polycentropus pentus, Polycentropus maculatus,* and a species of Hydroptilidae emerged early in the summer and had completed their emergence by July 17 in both years and thus did not provide information on the effect of an intermittent flow on the fauna. *Lepidostoma grisea* (figure 7), *Cheumatopsyche pettiti, Chimarrha aterrima,* and *Polycentropus confusus* emerged after July 17 in 1939, but did not emerge in this period in 1938. Thus this group consists of species which were eliminated when the stream became dry.

Discussion

It has been demonstrated, especially for the Plecoptera, Ephemeroptera, and Trichoptera but also for the Chironomidae, that the aquatic stages of insects belonging to these groups are eliminated entirely or reduced numerically when a stream dries up. The first three groups have a low tolerance for conditions associated with an intermittent flow and were either killed or forced to migrate from the area as the drying became complete, while the last group seemed to withstand or avoid desiccation, at least to some degree. Since many of the Chironomidae are known to dwell in the small interstices of the bottom particles, it is probable that these were able to retreat to moist areas under large rocks and here obtain sufficient moisture to complete the aquatic portion of their life-cycles. The numerical reduction observed in the emergence of this group after July 17 in 1938 as compared with that of the same period in 1939 probably represents the number unable to secure such suitable microhabitats.

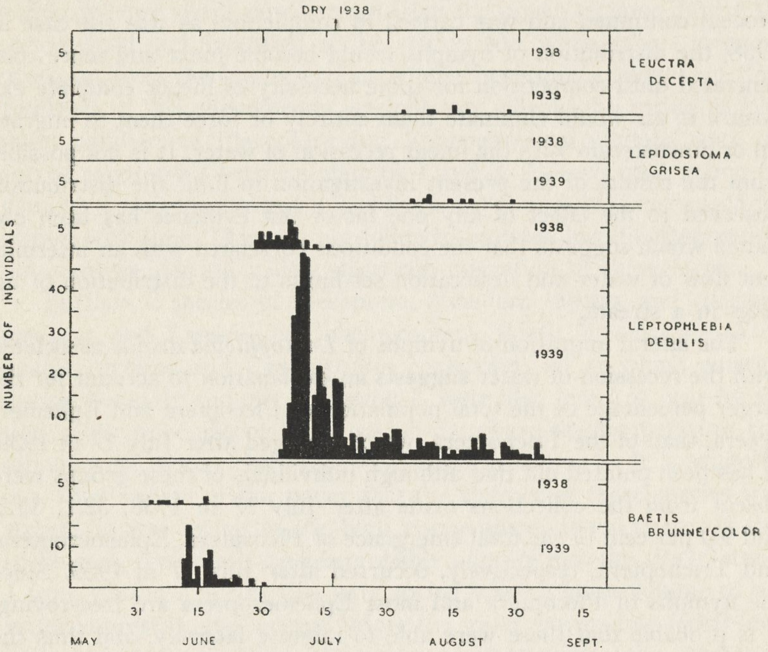

Fig. 7. Emergence polygons of representative species at station 1 in 1938 and 1939, showing the effect of the drying up of the stream on July 17th, 1938, on the insect emergence.

It was observed during the summer low-water period in 1939 that nymphs of *Leptophlebia debilis,* a species that was eliminated by the drying in 1938, moved gradually towards the centre of the stream as the water receded from the margins. Thus the number of nymphs per unit area increased in the mid-channel and the original wide distribution over the whole stream bed was changed to a concentrated distribution where the conditions were most favourable. If the drying process continued and was carried to completion, as was the case in 1938, the distribution of nymphs would become more and more concentrated until competition for some necessity of life or complete exposure to air would eliminate them entirely or force them to migrate up or downstream with the linear recession of water. It is not possible from the results of the present investigation to limit the distribution observed to the effect of any one factor but evidence has been obtained which suggests that the conditions correlated with an intermittent flow of water and desiccation set limits to the distribution of insects in a stream.

The lateral migration of nymphs of *Leptophlebia debilis* associated with the recession of water suggests an explanation to account for the larger percentage of the total population of Plecoptera and Ephemeroptera, than of the Trichoptera, which emerged after July 17 in 1939. It has been pointed out that although individuals of these groups were absent from the collections made after July 17 in 1938, 32.1, 35.2, and 9.0 per cent of the total emergence of Plecoptera, Ephemeroptera, and Trichoptera, respectively, occurred after July 17 in 1939. Since the nymphs of Plecoptera and most Ephemeroptera are free-roving, it is probable that these were able to migrate laterally, and thus the majority of the population was able to survive in the reduced stream channel during the period of low water in 1939. The Trichoptera, however, showed a much lower survival for the same period than either the Plecoptera or Ephemeroptera. This may be explained by the fixed habit of many larvae and pupae of this group which would prevent or hinder lateral migration as the water receded and thus only those individuals originally situated on the lower bottom particles in the mid-channel would survive.

Although only scattered information was obtained regarding the repopulation of the stream in 1939 following the drying in 1938, it is interesting to speculate on this problem and several possibilities arise. Probably some eggs deposited in the early summer of 1938 were able to withstand desiccation and thus hatch and complete the life-cycle during the late summer and following spring when a flow was restored to the stream. Also late summer oviposition in 1938 would not be affected since a small flow was present at that time. However, these possibilities are not sufficient to account for certain elements of the population found in 1939. It is probable that some individuals were swept downstream from the upper sections during the spring flood and deposited at the station site, while others migrated upstream from the lower sections where there was a permanent flow. Evidence of this phenomenon was obtained during the spring of 1939 when numbers of Plecoptera and Ephemeroptera nymphs were observed at intervals between stations 1 and 2. At each observation the nymphs were concentrated in a different area and this progressed upstream with time. This was not followed in detail but the observations did seem to indicate a slow upstream migration of these forms.

Further, 2 species of Plecoptera, *Nemoura serrata,* and *Alloperla mediana,* and 3 species of Ephemeroptera, *Baetis brunneicolor, Stenonema carolina* and *Centroptilum convexum,* all of which emerged during the early summer at station 1, were also found at near-by station 2 but were absent from station 3a where the temperature conditions were more closely related to those at station 1. It is suggested in a later section of this paper that the absence of these species from station 3a was owing to the high temperatures found there. If such is the case, then these species probably migrate into the site of station 1 from station 2 during the early spring when a large volume of cold water is present, and emerge before the water warms to a lethal level. This faunal composition of station 1 substantiates the suggestion of migration as an active factor restoring the population to this area each year. Stehr (1938) reports that migration is an important factor in the restoration of the insect fauna to an intermittent stream. That the immature stages of certain aquatic insects are capable of extensive migrations, has been proved by Neave (1930) in a report of the movements of nymphs of *Blasturus cupidus* (Ephemeroptera).

A total of 26 species belonging to the Plecoptera, Ephemeroptera, and Trichoptera were found at station 1. This was much lower than the number found at stations 2, 3a, 3, and 4, which also were characterized by a rubble bottom but had a permanent flow. It was found that the number of species at these stations was correlated with the average summer temperatures in the stream (page 68), while the number at station 1 did not follow this correlation. In comparison with the 26 species found at station 1, there were 37 species at station 2 which was located close to station 1 but had a much lower temperature, and 48 species at station 3a where the temperature conditions approximated those at station 1. This lack of correlation resulted from the limitations to the success of aquatic insects associated with an intermittent flow. In such streams a highly variable type of habitat is presented to the insect population and to survive they must be able to withstand or avoid diverse physical conditions such as freshets, still water and desiccation. The greater number of species found at station 1 in 1939 showed that, although a large number of species may be present each year, only the most tolerant forms and those that emerge early in the season are able to complete their life-cycles in the stream when conditions become severe as was the case in the summer of 1938.

The Effect of Flooding by a Beaver Dam on the Insect Fauna of a Rapids

The construction of the beaver dam at the end of June in 1939 transformed the shallow rocky rapids, in which station 3 was located, into a deep sedimented pool. Thus a natural field experiment was set up which provided a considerable amount of information regarding the tolerance of different insect species to varied conditions of current and type of bottom.

These observations have already been published (Sprules, 1941) but because of their interest here will be briefly discussed below.

There was a decrease in the total number of insects taken in the traps as the station changed from a lotic to lentic environment, which could not be explained on the basis of annual variation. Not only was there a change in numbers but also in the proportions of the species in the catch. The Ephemeroptera which constituted about 56 per cent of the catch in 1938 decreased to 46 per cent in 1939 and to 12 per cent in 1940. Similarly the Plecoptera diminished from 2 per cent to about 0.2 per cent. The Trichoptera also dropped about one-quarter of the initial representation. On the other hand the proportion of Chironomidae increased from 31 per cent in 1938 to 84 per cent in 1940.

With respect to the productivity of this area, the effect of the numerical reduction is more pronounced when the volume or weight of the annual emergence is considered. Both the immature and adult stages of the Ephemeroptera, Trichoptera, and Plecoptera groups, which accounted for most of the reduction, are larger and heavier forms than the corresponding stages of the Chironomidae, which is the only group that increased consistently following the introduction of lentic conditions.

Further examination of the material showed that the changes were the result of a differential effect on species. Of the Ephemeroptera, Trichoptera, and Plecoptera, a total of 33 species were wiped out or reduced numerically in the lentic period, 15 species showed no appreciable change in emergence and 10 species appeared at the station during that time. These data indicate the existence of three main groups of species including typical lotic inhabitants which were unable to tolerate the lentic conditions, tolerant species which were able to adjust themselves to either lotic or lentic environments and lentic species which were unable to tolerate lotic conditions.

As a group, the Plecoptera consisted of typical rapid-water dwellers since 9 species were eliminated following construction of the dam, 1 species emerged throughout the investigation, and there were no new species introduced when the pool conditions prevailed. The Ephemeroptera showed a wider range of habitat tolerance since 14 species were eliminated, 7 emerged each year and 7 species were found at the station only after the end of June in 1939. Of this last group some of the species emerged from the area during the late summer of 1939, indicating that the immature stages migrated into the area immediately following the establishment of lentic conditions. Ten species of Trichoptera were eliminated, 7 species emerged under both sets of conditions and 3 species occurred only in 1940. The lack of any new species in the late summer period of 1939 indicates that the immature stages of this group did not migrate as readily as the Ephemeroptera and probably were dependent on oviposition in 1939 to become established in the lentic environment.

The numerical reduction of emergence and subsequent elimination of the typical rapid-water species occurred immediately after the environmental conditions were altered in 1939. In some instances species which were emerging in quantity prior to the flood were entirely absent from the collections made five days after its inception. Although representatives of the still-water fauna did enter the area during the late summer of 1939, the fauna was not established in numbers until the following year.

The decrease in rate of flow, increase in depth, and change in the type of bottom caused by the deposition of silt and other particulate matter over the rubble as the transport power of the stream was reduced were associated with quantitative and qualitative changes in the insect fauna. These three physical factors are closely interrelated in streams and it is difficult to determine the role played by any one of these in limiting the distribution of the insect fauna.

It has been shown that species exhibit different degrees of habitat tolerance in streams. The species that were eliminated from the rapids when it was transformed into a pool showed a narrow range of tolerance and were species typically associated with riffle areas. Species that were present in the area under both sets of conditions were forms that showed a wide range of tolerance and were found in several different habitats in the stream. Degrees of tolerance were exhibited by the species of this group since some emerged in smaller numbers in the lentic than in the lotic habitat while others emerged in equal numbers in both habitats. The species that emerged from the area only during lentic conditions showed a narrow range of tolerance and were types that were typically found in still-water habitats.

It is probable that the reduction in current was of importance in the elimination of rapid-water species. Many of these are dependent on current for respiration and others, such as the net-building Trichoptera, are of fixed habit and depend on current to wash food material into the nets. Further, the deposition of silt which accompanied the reduction of flow would injure the gills of certain species and lead to suffocation in some instances. Many of the free-living species could migrate from the area when the environmental conditions became severe, while others of fixed habit would be unable to avoid the new conditions.

A wide variety of microhabitats is found in rapids where the bottom consists of rocks and rubble. Thus species that show preference for a rapid flow and for rubble bottom would find suitable niches, while in the lee areas species that prefer reduced current or even quiet water, and gravel or sand bottoms, also would find suitable niches. The latter species are those that showed a wide range of habitat tolerance in this investigation and survived under lentic conditions. The decrease in the number of different microhabitats that accompanied the change of bottom could account for the associated decrease in the diversity of the fauna.

It would seem that current was the most important factor limiting the distribution of the typical quiet-water species. The rapidity with which some of these types entered the area once lentic conditions were established indicates that they were continually attempting to extend their distribution but were not successful until conditions were such as to allow fulfilment of this tendency. The lack of morphological adaptations in these species to withstand a rapid flow would prohibit their establishment in running water. Other factors, such as the increase in amount of organic food material deposited on the rubble when the current was reduced and the reduction of predators through the elimination of rapid-water species, were probably of minor importance in the successful extension of the distribution of these species.

The Insect Distribution on Different Types of Bottom

The smaller streams of Algonquin Park are characterized by the presence of many different types of bottom and several of these often are found in close proximity to one another in a short section of stream. An investigation of the insect fauna associated with different types of bottom was carried out to determine the relationship between size of bottom particles and the existing insect distribution.

During this study two uncontrollable contingencies arose which altered the physical nature of certain stream areas under investigation as well as the normal insect populations, and have made it difficult to make comparative analyses of the data. The first of these was the sudden freshet in 1940 which affected the insect emergence at stations 6 and 7 and may have affected that at station 3a, although this cannot be stated definitely since this station was not in operation prior to 1940 to allow a comparison of results. The second event was the construction of the beaver dam below station 3 in 1939, the effects of which have been discussed in the previous section. These are natural disturbances with which an ecologist is faced frequently in Algonquin Park and the new conditions presented in these instances must be accepted. Although the freshet and beaver dam provided a considerable amount of valuable information on factors affecting insect distribution in streams, they nevertheless disrupted certain of the original plans and have made the interpretation of results more difficult through the addition of extra variables.

Quantitative Results

The number of insects that emerged from different types of bottom in 1938, 1939, and 1940 was determined and the results have been summarized in table 5. In each year the emergence from the sand bottom was numerically less than that from any other type of bottom. Conversely it was found that rubble bottoms with a rapid flow of water produced the greatest insect emergence in 1939 and 1940, while in 1938 an exception to this occurred, since in the period sampled 1,942 insects were collected from the gravel-bottom station and only 1,677 from the rubble. This discrepancy was the result of an error introduced in connection with the method of collecting employed at station 6 in 1938 (page 18). From the collections obtained at station 3, following the building of the beaver dam which transformed the riffle into a pool at the end of June 1939, it was found that a rubble bottom in deep pool conditions produced a smaller number of insects than the rapid-water type. The gravel and muck bottoms were intermediate between the rubble and sand bottoms from the standpoint of total insect emergence. In 1938 and 1939 the gravel produced more insects than the muck, while in 1940 the relation was reversed. This latter instance resulted from the freshet (page 24) which scoured the gravel section, reducing the population considerably, while it had little if any effect on the population at the muck station.

In order to compare the quantitative results of this study more directly, the total insect emergence in each year from the different types of bottom was converted into a ratio with the emergence from sand bottom as the unit. The average values of the ratios for the complete period of the investigation were rubble (rapid) 4.6, rubble (pool) 3.3, gravel 2.1, muck 1.8 and sand 1.0 showing a decreasing productivity of insects from rapid rubble areas to sand.

Results obtained in the present investigation correspond closely to those of other investigators. Needham (1927) found a decrease

Table 5.—Analysis of the total insect emergence from different types of bottom in 1938, 1939, and 1940.

	1938 27 daily collections from June 29 to September 18				1939 Daily collections from June 6 to September 11			1940 Daily collections from June 1 to August 31				
Station........	No. 3	No. 6	No. 5	No. 7	No. 6	No. 5	No. 7	No. 3	No. 3a	No. 6	No. 5	No. 7
Type of bottom.	rubble (rapid)	gravel	muck	sand	gravel	muck	sand	rubble (pool)	rubble (rapid)	gravel	muck	sand
Ephemeroptera..	952	57	283	25	195	608	385	469	1,035	64	142	29
Trichoptera	172	26	44	14	36	57	16	102	270	36	109	20
Plecoptera	34	41	0	7	105	0	7	7	450	13	1	5
Chironomidae ..	480	1,753	859	598	2,131	1,270	1,379	3,227	3,446	620	1,936	786
Simuliidae	0	22	0	2	604	0	10	4	1,554	604	0	18
"Miscellaneous"	40	43	23	24	95	21	3	10	478	32	3	44
Total.......	1,677	1,942	1,208	670	3,166	1,956	1,832	3,819	7,233	1,369	2,191	902

in the standing crop from rubble through gravel, muck, to sand. Tarzwell (1936) carried out an extensive survey of many grades of bottom in the streams of Michigan and found an increase in population rating from sand to bottoms supporting various aquatic plants. Tarzwell's results converted into ratios give rubble 3.6, gravel and sand 2.6, mucky flats 2.3 and sand and silt 1.0. These agree very closely with those of the present study.

Numbers of individuals are of course not always the best indication of the biomass. A few determinations of the volume of insects produced by different types of bottom were made and from these it was found that the bottoms were related with respect to volume of emergence in the same order as when the number of insects was considered. The ratios obtained from the rubble (rapid), gravel, muck, and sand bttoms were respectively 20.7, 3.6, 1.5 and 1.0. The apparent lack of correlation between volume (20.7) and numbers (4.6) at the rubble station resulted from the preponderance of insects with a relatively large body size, such as Plecoptera, Ephemeroptera, and Trichoptera, which were found in this habitat.

Qualitative Results

(*a*) *General differences.* There are major qualitative differences in the insect emergence at stations associated with different types of bottom in a stream. In order to analyze these differences the number of insects belonging to each of the main groups that emerged from different types of bottom has been expressed as a percentage of the total annual emergence. The average percentage composition of the fauna associated with each type of bottom was determined for the complete period of the investigation (table 6).

Table 6.—Average per cent composition of the insect emergence from rubble (rapid), gravel, muck, and sand bottoms, for 1938, 1939, and 1940.

	Rubble (rapid)	Gravel	Muck	Sand
Ephemeroptera	35.5	4.6	20.3	9.3
Trichoptera	7.0	1.7	3.8	1.7
Plecoptera	4.1	2.1	0.0	0.7
Chironomidae	38.2	67.6	74.8	83.9
Simuliidae	10.8	21.4	0.0	0.9
"Miscellaneous"	4.4	2.5	1.0	3.5

Sand. The emergence from the sand bottom consisted for the most part of Chironomidae which made up the greatest proportion of the population each year and averaged 83.9 per cent for the complete period of study. The Ephemeroptera was the next most abundant group averaging 9.3 per cent of the total emergence. The "Miscellaneous," Trichoptera, Simuliidae, Plecoptera followed in order, representing in each case only a small element of the total emergence.

Muck. The emergence from the muck bottom consisted predominantly of Chironomidae which averaged 74.8 per cent of the total emergence over the complete period of the study. The Ephemeroptera was the next most abundant group, averaging 20.3 per cent of the total. Thus the total component of Chironomidae and Ephemeroptera, the two most prevalent groups, was almost identical at the sand and muck stations. The diminution in the percentage of Chironomidae at the muck site as compared with that at the sand was compensated for by an increase in the percentage of Ephemeroptera. The Trichoptera and "Miscellaneous" followed in order of relative abundance. The Simuliidae and Plecoptera[2] groups were not represented at the muck station; this was the most significant faunal difference noted between this station and all others.

Gravel. The emergence from the gravel bottom also consisted for the most part of Chironomidae, which averaged 67.6 per cent of the total emergence during the investigation. The Simuliidae made up a considerable portion of the emergence at this station, averaging 21.4 per cent. The Ephemeroptera, "Miscellaneous," Plecoptera, and Trichoptera followed in order of decreasing numbers and contributed only a small element to the total emergence in each instance. The increased proportion of Simuliidae was the most significant difference observed in the emergence from the gravel bottom as compared with that from sand and muck bottoms.

Rubble. At the rapid rubble bottoms the emergence consisted of more equal proportions of all the insect groups than were found at any other type of bottom. Once again the Chironomidae formed the most abundant element, averaging 38.2 per cent of the total, while the Ephemeroptera followed closely with 35.5 per cent. The Simuliidae averaged 10.8 per cent of the total, and the Trichoptera, Plecop-

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[2] One individual taken in 1940—likely washed in following high water.

tera, and "Miscellaneous" followed in decreasing order of abundance, each group making up a larger proportion of the total emergence than was found at any of the other types of bottom.

Table 7.—Total number of species of Plecoptera, Ephemeroptera, and Trichoptera that emerged from different types of bottom during the investigation.

	Total number of species	Rubble	Gravel	Muck	Sand
Plecoptera.......	11	11	8	1	5
Ephemeroptera...	34	21	18	19	14
Trichoptera......	27	22	12	15	11
Total.......	72	54	38	35	30

(*b*) *Species differences.* The distribution of species belonging to the Plecoptera, Ephemeroptera and Trichoptera on the different types of bottom was determined. When the total number of species was considered, it was found that 54 emerged from rubble, 38 from gravel, 35 from muck, and 30 from sand (table 7). Thus with respect to the three groups in which species determinations were made, the diversity of the fauna decreased from rubble through gravel and muck to sand. This is the same sequence as was found when the total number and volume of all insects were considered.

Plecoptera. The Plecoptera were represented at the stations by 11 species, all of which were found at the rubble bottom, 8 at gravel, 5 at sand and 1 at muck, which was represented by a single individual (table 8). There were 3 species found only on the rubble bottom; 1 species was common to rubble, gravel, and muck; 2 were confined to rubble and gravel; while 5 species were common to rubble, gravel, and sand. Thus the most diverse population was associated with rubble bottoms followed in order by gravel, sand, and muck.

The distribution of species and the relative abundance of each species on different types of bottom indicated that the preferred habitat for this group was rubble riffle areas. Although there were only 3 species found in the rubble that were not found in the gravel, in almost every case the relative abundance of each species was less in the gravel area. In every instance the relative abundance of the species found on the sand bottom was less than on the rubble or gravel bottoms. The Plecoptera population was negligible on the muck bottom, indicating that the conditions associated with such a habitat are unsuitable for the stonefly fauna found in this stream. This was substantiated by observations made at station 3 in 1939 and 1940 when the rubble riffle was converted into a still pool by a beaver dam. It was found that the Plecoptera disappeared from the area, with the exception of *Isoperla sp.1* which remained in reduced numbers (Sprules, 1940). Frison (1935) found that although the Plecoptera of Illinois were found in many diverse habitats only one species, *Isoperla minuta* Banks, was confined to small muddy-bottomed streams.

Table 8.—Distribution of Plecoptera and relative abundance of each species on different types of bottom. A—over 50 individuals; F—10 to 50; R—1 to 10; T—1 individual. The abundance represents the maximum annual emergence obtained during the investigation.

	Rubble (rapid)	Gravel	Muck	Sand
Leuctra decepta	A	F		R
Leuctra tenuis	A	F		R
Isoperla sp. 1	F	F		R
Isoperla montana	R	F		T
Hastaperla brevis	R	R		T
Isoperla truncata	F	R		
Alloperla imbecilla	R	F		
Nemoura venosa	F	R	T	
Leuctra hamula	F			
Leuctra sibleyi	R			
Acroneuria abnormis	R			
Total	11	8	1	5

Ephemeroptera. The Ephemeroptera were represented by 34 species, of which 21 were found at the rubble stations, 18 at the gravel, 19 at the muck, and 14 at the sand station (table 9). Species that were represented by female imagos only have not been considered in preparing the species list for each station (page 44). There were 5 species confined to rubble, 3 to gravel, and 5 to muck, while no

TABLE 9.—Distribution of Ephemeroptera and relative abundance of each species on different types of bottom. A—over 50 individuals; F—10 to 50; R—1 to 10; T—1 individual. The abundance represents the maximum annual emergence obtained during the investigation.

	Rubble (rapid)	Gravel	Muck	Sand
Baetis cingulatus	F			
Epeorus humeralis	R			
Leptophlebia guttata	R			
Heptagenia hebe	R			
Baetis parvus	T			
Leptophlebia mollis	A	F		
Ephemerella invaria	T	R		
Pseudocloeon carolina	R	T		
Stenonema fuscum	F	T	R	
Habrophlebia vibrans	A	F	A	F
Ephemerella sp. (*bicolor* gr.)	R	R	F	F
Stenonema rubromaculatum	F	R	F	R
Leptophlebia debilis	A	R	R	R
Baetis flavistriga	A	R		R
Heptagenia pulla	A	F		T
Baetis pluto	A	A		R
Baetis sp. (*pygmaeus* gr.)	A	F		R
Centroptilum simile	R		T	R
Stenonema ?vicarium	R		R	
Stenonema canadense	F		R	
Leptophlebia volitans	F		R	
Baetis frondalis		R	T	R
Centroptilum semirufum		R	R	A
Centroptilum convexum		T	F	F
Ephemerella deficiens		F		
Ephemerella sp. (near *serrata*)		T		
Baetis vagans		T		
Cloeon triangulifer			R	R
Caenis sp.			F	T
Cloeon simplex			R	
Cloeon rubropictum			R	
Brachycercus sp.			R	
Blasturus sp.			R	
Ephemerella lutulenta			T	
Total	21	18	19	14

species were found at the sand station alone. Four species were common to all the habitats; 4 to rubble, gravel, and sand; 1 to rubble, gravel, and muck; 3 to rubble and gravel; 3 to rubble and muck; 1 to rubble, muck, and sand; 3 to gravel, muck, and sand; 2 to muck and sand. Thus the most diverse population was found on the rubble bottoms followed by muck, gravel, and sand in decreasing order.

The distribution of species on different types of bottom showed that the species of Ephemeroptera had a much wider range of habitat preference than the Plecoptera. The distribution of species and the relative abundance of individuals on the different types of bottom indicated the habitat preference of each species and the range of habitats it could tolerate. For example, *Heptagenia pulla* occurred abundantly on rubble, frequently on gravel, was represented by a single individual on sand, and did not occur on muck (table 9). Thus, for this species, preference is shown for conditions associated with rubble bottoms, followed closely by gravel, and, although able to tolerate sand conditions, it is unable to tolerate conditions prevailing in a muck habitat. Although no species were found only at the sand station, when the relative abundance of individuals found on the different types of bottom was considered, it was found that certain species such as *Centroptilum semirufum* showed a distinct preference for sand since the maximum emergence occurred there.

Trichoptera. The Trichoptera were represented at the stations by a total of 27 species, of which 22 were found on the rubble bottoms, 12 on the gravel, 15 on the muck, and 11 on the sand bottom (table 10). There were 5 species confined to rubble, 4 species to muck, while none were found only on the gravel or sand bottoms. There were 4 species common to all the habitats; 4 to rubble, gravel, and sand; 2 to rubble, gravel, and muck; 2 to rubble and gravel; 3 to rubble and muck; 1 to rubble and sand; 1 to rubble, muck, and sand; 1 to muck and sand. Thus this group showed the same general distribution as the Ephemeroptera, since the most diverse fauna was found on rubble, followed by that on muck, gravel, and sand in decreasing order.

The Trichoptera showed a wider range of habitat preference than the Plecoptera but not as wide as the Ephemeroptera, since there were no species confined to either the gravel or sand habitats. In fact, all the species found on the gravel bottom were found on the rubble bottom and in no instance was the relative abundance of a species greater in the gravel than in the rubble area. Thus the gravel fauna consisted almost entirely of species that showed a preference for the rubble habitat but were able to extend their distribution into a gravel riffle. In the same way the sand fauna consisted in general of species which were found in a rubble riffle where the relative abundance was at least as great. Two exceptions occurred to this generalization.

TABLE 10.—Distribution of Trichoptera and relative abundance of each species on different types of bottom. A—over 50 individuals; F—10 to 50; R—1 to 10; T—1 individual. The abundance represents the maximum annual emergence obtained during the investigation.

	Rubble (rapid)	Gravel	Muck	Sand
Cheumatopsyche campyla	R			
Lepidostoma grisea	R			
Neophylax autumnus	R			
Psychomyella flavida	R			
Agapetus sp.	R			
Rhyacophila fuscula	R	R		
Athripsodes angustus	R	R		
Nyctiophylax vestitus	F	R	F	
Phylocentropus placidus	T	T	T	
Plectrocnemia cinerea	R	R	F	R
Psychomyia diversa	R	R	F	R
Cheumatopsyche pettiti	F	R	T	R
Hydroptilidae	T	T	T	R
Philopotamus distinctus	A	R		T
Chimarrha aterrima	A	F		R
Hydropsyche sparna	F	R		R
Hydropsyche betteni	F	F		R
Stenophylax guttifer	R		R	T
Polycentropus confusus	R		R	
Athripsodes dilutus	R		R	
Mystacides sepulchralis	R		F	
Rhyacophila carolina	R			T
Oecetis inconspicua			F	T
Lepidostoma costalis			F	
Pycnopsyche aglonus			R	
Platycentropus indicans			R	
Molanna sp.			T	
Total	22	12	15	11

First, one species found on sand, *Oecetis inconspicua,* was not found on rubble, and from its maximum abundance showed a habitat preference for muck bottom. Thus this species is probably a still-water form which was able to tolerate the conditions prevailing at the sand station but unable to extend its distribution to either the gravel or rubble bottoms where a considerable current existed. Second, the family Hydroptilidae showed its maximum relative abundance on the sand bottom although it was present at all the habitats and thus, as a group, must be considered one which shows a habitat preference for sand but can tolerate the conditions prevailing at a variety of habitats. If complete species identification had been made in this family it is probable that a more diverse distribution would have been obtained for it.

The Trichoptera are known to occupy a wide range of habitats. Certain families, such as the Phryganeidae, are found in still water or slow-flowing habitats, while others, such as the Rhyacophilidae, are limited to rapid streams. Siltala (1906) found several species in the Bay of Finland living under marine conditions and utilizing marine algae for food and larval cases, while one European species, *Enoicyla pusilla* Burmeister, is known to be terrestrial.

Discussion

It is probable that, other things being equal, current is of prime importance in limiting the distribution of aquatic insects in a restricted section of a stream. Wingfield (1939) found that in certain aquatic insects the demand is for current which continually brings a fresh supply of oxygenated water to the respiratory surface rather than for a high dissolved oxygen content as formerly held (Hubault, 1927), and that in some species of Ephemeroptera the gills are used to create a current over the body and are used as secondary respiratory organs only when the oxygen content of the water is extremely low. This could account for the inverse correlation between the gill area of Ephemeroptera nymphs in mountain streams and the dissolved oxygen content found by Dodds and Hisaw (1924b). Wu (1931) found that the Simuliidae had an "inherent current demand" and this was substantiated in the present investigation by the absence of this group from station 5 where the current was negligible. The Plecoptera were also absent from this station and it is probable that this distribution was related to current also, since gill development in these forms is slight and current cannot be satisfactorily developed mechanically. The Ephemeroptera, Trichoptera and Chironomidae, as groups, were not so directly limited by current since there were different species associated with different currents.

Many aquatic insects in streams are dependent on current for food supply and it is probable that this condition is important in limiting the distribution of such forms. Clemens (1917) found that the nymphs of *Isonychia bicolor* (Ephemeroptera) were not dependent on current for oxygen supply but did utilize current to supply food. In this form suspended organic materials of the stream were strained out by means of fringes of hairs on the forelegs. In many of the Trichoptera, such as the net-building Hydropsychidae, the larvae are dependent on current for food supply.

Thus certain species which are normally found in rapid-water habitats would be unable to establish themselves in still-water habitats because of limitations to respiration and feeding set by the reduced current. At the other extreme, typical still-water species would be unable to withstand a rapid flow because of the lack of suitable morphological adaptations. Between these extremes there are many species which show a wide range of current tolerance but in almost every instance the number of individuals decreases as these species approach the limits of their tolerance in different habitats.

The nature of the bottom, which is also of considerable importance in limiting the distribution of insects in a stream, is so closely related to current that it is difficult to discuss these separately. There is a reciprocal relation between the two since bottom primarily is determined by current and the current markedly affected by bottom.

The rapid rubble habitat provides within itself many microhabitats with diverse conditions which may well account for the diverse composition of the fauna found there. Thus the species that require a rapid current and those preferring rubble bottom would find optimal conditions in such a habitat while those that prefer a reduced current and sand or gravel bottom would be able to find such niches in the lee of the larger rocks and rubble. Here, then, a diverse fauna could exist, while in gravel sections the variety of available microhabitats would be reduced, thus limiting the diversity of the associated fauna. There would be little variation in the types of microhabitats available on sand bottoms and this fact, coupled with the decreased current in such areas would result in a restricted fauna of bottom sprawlers and small forms which could utilize the interstitial spaces between the particles. The muck habitat would not support any forms requiring a rapid rate of flow and the population would consist of typical still-water sprawlers and burrowing forms. Thus the variety of available microhabitats in any area may limit the diversity of the associated insect fauna.

Further, the size and configuration of bottom particles would determine the amount of cover available for species of different body size and this factor may set other limits to the distribution of species. The rubble habitat provides suitable cover for even the largest insects, while the various microhabitats provide cover for a diverse population of smaller forms. Large forms would also find suitable cover in gravel areas although the numbers of such niches would be reduced. On sand beds there would be no cover available for large forms and only the smallest insects would be able to utilize the interstitial spaces. Thus in general the diversity of available cover decreases as the size of the bottom particles decreases. One exception to this generalization occurs in that muck bottom, which primarily consists of smaller particles than sand bottom, often contains a considerable amount of decaying vegetable matter and even large insects could obtain cover under twigs and leaves. Mottley et al. (1938) pointed out the tendency toward heterogeneity, with a great increase in the number of potential habitats for organisms at different levels, where the bottom consisted of large particles.

Linduska (1942) studied the habitat preference of certain species of Ephemeroptera in Rattlesnake creek, Montana, and found that in general they had well-defined requirements for a given type of bottom and that the local distribution in the stream was limited by the nature of the bottom.

The results of the present investigation agree completely with this. Further, he states, "stream flow, as such, appeared to be of no appreciable consequence in limiting local distribution, and most species were observed capable of inhabiting situations under a wide range of surface velocities wherever acceptable bottom types occurred." Linduska considers type of bottom of prime importance in limiting the local distribution of the forms he studied, and rate of flow of secondary importance. In the present study it has been found that current and nature of the bottom particles are intimately interrelated and the separate effect of these factors on the distribution of insects in the streams of Algonquin Park could not be distinguished.

Another factor which must be considered when the composition of the fauna is determined for some specific area in a stream is the proximity of one type of bottom to another. Thus in this investigation the muck bottom was situated only a few feet downstream from the rapid rubble station. It is probable that this would allow an influx of insects from the rapids to the muck habitat since certain individuals would be swept down, at intervals, by the current. This was substantiated during the study, since in 1938 and early in 1939 large numbers of *Habrophlebia vibrans* emerged both at the muck and rubble stations. However, when the rapids was converted into a pool in 1939, the number of individuals at both sites was greatly reduced showing that this species was normally associated with a rapid rubble habitat and, although able to survive in the muck, this was not the preferred habitat. The same condition could have existed at the sand station since it was situated in close proximity to the gravel riffle. Thus it is probable that the nature of the stream bottom in the surrounding area, especially in the upstream portion, may have a bearing on the fauna found at any specific site in a stream.

It has been pointed out that the diversity of the insect fauna in any area is related to the number of different microhabitats present in that area. This factor also probably limits the number of individuals in the area, at least to some degree. However, another factor which may limit the number of insects found in any area is the utilizable surface area of bottom particles exposed to the water. It was found that the number of insects that emerged from different types of bottom decreased from rubble, through gravel and muck, to sand. The rubble area provided the greatest area of bottom particles exposed to the water and this was followed by gravel, muck and sand where the utilizable surface area decreased, in order, from the standpoint of aquatic insects. The presence of decaying organic matter on the muck bottom increased the surface area exposed to the water in this habitat.

In the consideration of surface area exposed to the water, the size of organisms must be taken into account. Thus, although few aquatic insects found in streams could utilize the interstitial spaces in a sand bottom, it has been shown by Pennak (1939) that there is an extensive microfaunal population (Rotifera) found in sandy lake shores. These forms are of small body size and are able to utilize the interstices.

In addition, it is probable that the amount of organic food material limits the number of organisms found in any area and should be considered along with the utilizable surface area of bottom particles exposed to the water.

Tarzwell (1936) carried out an extensive study of the bottom fauna of different types of bottom in a stream and considered many intergrades such as coarse, medium and fine gravel along with various types of aquatic plant beds. The results showed an increase from sand, which was given a population rating of 1, up to beds of *Elodea sp.,* which had a rating of 452. This high population rating could be explained by the original premise since plant beds would afford an enormous surface area exposed to the water as well as an abundant supply of organic food material. Needham (1927) found hardpan and bedrock areas to be less productive than sand. Here the surface area of bottom particles exposed to the water, available cover and amount of organic material present would be minimal. From a few collections made from an area in the Madawaska river where the bottom consisted of large boulders it was found that the population was much lower than that found in the areas of small rubble and rocks. Once again, since the interstitial spaces are reduced in number as the rocks increase in size, such areas would present a less favourable habitat if surface area were considered.

It may therefore, be postulated from such data that there is a direct relationship between the utilizable surface area of bottom particles exposed to the water and the productivity of aquatic insects. Mottley et al (1938) suggested that the number of organisms per unit of substratum exposed to the water might give a better measure of the richness of a stream than the number per unit area of bottom.

Wene and Wickliff (1940) carried out an experiment in Blacklick creek, Ohio, in which the results offer direct substantiation of the above postulation. Wire baskets were filled with denuded medium and small rubble and placed in the creek bottom so that the surface of the rubble was level with the surrounding bottom. When the baskets were placed in a sandy bottom pool it was found that in February, 1938, after the baskets had been in position for approximately one month, the small rubble had about three times and the large rubble five times as many insects as the corresponding check samples from the surrounding sand bottom.

A field observation which further illustrates the relation of surface area of bottom particles and the number of insects may be obtained from observations of the distribution of groups which have a narrow range of habitat preference (such as the Simuliidae and the net-building Trichoptera) where their aggregation in localized positions on the stones may be readily seen.

It was found that the distribution of insects in a stream showed quantitative and qualitative differences which were associated with different types of bottom. It was not possible in this study to attribute these differences to the effect of any one condition that varied with the respective types of bottom, since the fact that the size of the bottom particles differed implies that there were corresponding differences in current, depth, volume of flow, light penetration, oxygen and carbon dioxide content, any one or all of which may play a significant role in limiting the distribution. However, since all these factors are interrelated, the phrase "type of bottom" may be used to represent the characteristics of the habitats referred to, although it must be realized that the various types of bottom cannot be laid down in a stream without accompanying alterations in other conditions. It is probable that the insect distribution found in this investigaton was the resultant of a complex interaction of several environmental conditions of which current and the nature of the bottom are relatively more important.

The Distribution of Insects in Rocky Riffles at Various Distances from the Source

A comparison of the insect emergence at stations 2, 3a, 3 and 4 was made to determine if there were quantitative and qualitative differences in the faunas which could be correlated with change in conditions downstream. These stations were selected at different distances from the source (figure 1) in rocky riffle areas in order to minimize the effect of other factors, such as type of bottom, which were known to affect insect distribution in streams.

The construction of the beaver dam (page 34) disrupted this investigation and made it impossible to compare the emergence at all the stations in any one year, since station 3a was not established until 1940 at which time the original rapids at station 3 had been transformed into a pool. However, it was found in several instances during this stream investigation that annual variation in insect emergence from any area is small. This is particularly true from the standpoint of the species emerging each year and thus the qualitative data probably have been affected only slightly by this circumstance. Although a portion of the differences observed, when comparisons are made of the quantitative data obtained from different stations in different years, may result from annual variation in emergence, it is improbable that the effect of this factor alone could account for all of the differences observed, and it is felt that such a comparison is of considerable value.

Quantitative Results

The total values for insect emergence from June 1 to August 31 at station 2 in 1939, station 3a in 1940, station 3 in 1938, and station 4 in 1939 illustrate the quantitative differences in the populations in rapids at different distances from the source (table 11). For the periods outlined above, a total of 5,393, 7, 175, 5, 440, and 31,505 insects

Table 11.—Quantitative analysis of the total insect emergence from June 1 to August 31 at station 2 in 1939, station 3a in 1940, station 3 in 1938, and station 4 in 1939.

	Station 2		Station 3a		Station 3		Station 4	
	No. of Insects	% of Total	No. of Insects	% of Total	No. of Insects	% of Total	No. of Insects	% of Total
Plecoptera......	663	12.3	450	6.3	116	2.1	122	0.4
Ephemeroptera..	502	9.3	1,035	14.4	3,037	55.8	1,820	5.8
Trichoptera.....	440	8.2	270	3.8	449	8.3	12,423	39.4
Chironomidae...	3,699	68.6	3,446	48.0	1,703	31.3	5,304	16.8
Simuliidae......	2	T	1,496	20.8	26	0.5	6,922	22.0
"Miscellaneous"	87	1.6	478	6.7	109	2.0	4,914	15.6
Total.......	5,393	100.0	7,175	100.0	5,440	100.0	31,505	100.0

emerged at stations 2, 3a, and 4 respectively. Thus the total emergence at the upper three stations showed only slight variation, while the emergence at station 4 was much greater than at any other station, although there was a considerable change in such conditions as width, depth, rate and volume of flow, and average temperature between each station. It was shown in the previous section that the number of insects found in any area is related to the utilizable surface area of bottom particles exposed to the water. This phenomenon is also clearly seen in this instance since the bottoms at stations 2, 3a, and 3 were similar, consisting of a few rocks imbedded in the underlying coarse gravel while at station 4, the bottom was made up of many rocks which were built up in layers with the bottom layer only imbedded.

However when the percentage of the total emergence at the various stations contributed by each of the main insect groups is considered, it is seen that there are changes in the relative importance of each group associated with distance from the source (table 11). The Plecoptera constituted 12.3, 6.3, 2.1, and 0.4 per cent of the total emergence at stations 2, 3a, 3, and 4 respectively. Thus this group made up an important part of the population near the source but decreased in relative importance downstream, until in the lower river region it constituted only a small proportion of the total population. The Chironomidae also decreased in relative importance downstream, dropping from 68.6 per cent of the total emergence at station 2 to 16.8 per cent at station 4. The Ephemeroptera constituted 9.3, 14.4, 55.8, and 5.8 per cent of the total emergence at stations 2, 3a, 3, and 4 respectively. The increase in relative importance of this group between stations 2 and 3 was accompanied by an increase in the number of individuals. At station 4 the number of individuals that emerged was greater than that at either station 2 or 3a, although it made up a smaller proportion of the total emergence than at the latter stations. Thus this group showed its maximum at station 3. The Trichoptera constituted only a small part of the population at the upper stations but was the most important single group at station 4 where it made up 39.4 per cent of the total emergence. The Simuliidae and "Miscellaneous" groups made up an appreciable portion of the total emergence at stations 3a and 4 but were of minor importance at stations 2 and 3.

Qualitative Results

TABLE 12.—Distribution of Plecoptera at stations 2, 3a, 3, and 4, showing the relative abundance of each species. A—over 50 individuals; F—from 10 to 50; R—from 1 to 10; T—1 individual. The abundance represents the maximum annual emergence for each station.

	Station 2	Station 3a	Station 3	Station 4
Leuctra sara	R			
Nemoura trispinosa	R			
Leuctra biloba	F			
Nemoura serrata	F			
Alloperla mediana	A			
Allocapnia pygmaea	R	R		
Nemoura venosa	F	F		
Leuctra decepta	A	F	F	
Nemoura punctipennis	F	R	R	
Leuctra sibleyi	A	A	R	
Leuctra hamula	A	A	F	
Isoperla montana	F	F	R	
Leuctra tenuis		A	A	
Isoperla sp. 1		F	F	
Alloperla imbecilla			R	
Isoperla truncata		F	R	A
Acroneuria abnormis		R	T	A
Hastaperla brevis			R	R
Isoperla transmarina				F
Acroneuria lycorias				R
Isoperla sp. 2				R
Hydroperla subvarians				T
Total	12	11	11	7

Plecoptera. The Plecoptera were represented by a total of 22 species of which 12 were found at station 2, 11 at station 3a, 11 at station 3, and 7 at station 4 (table 12). Thus, in general, the number of species decreased downstream as the distance from the source increased, and this was accompanied by a progressive change in the species comprising the fauna at each station. There were 5 species found only at station 2; 2 species confined to stations 2 and 3a; 5 species common to stations 2, 3a, and 3; 2 species confined to stations 3a and 3; 1 species found only at station 3; 2 species common to stations 3a, 3, and 4; 1 species confined to stations 3 and 4, and 4 species found only at station 4.

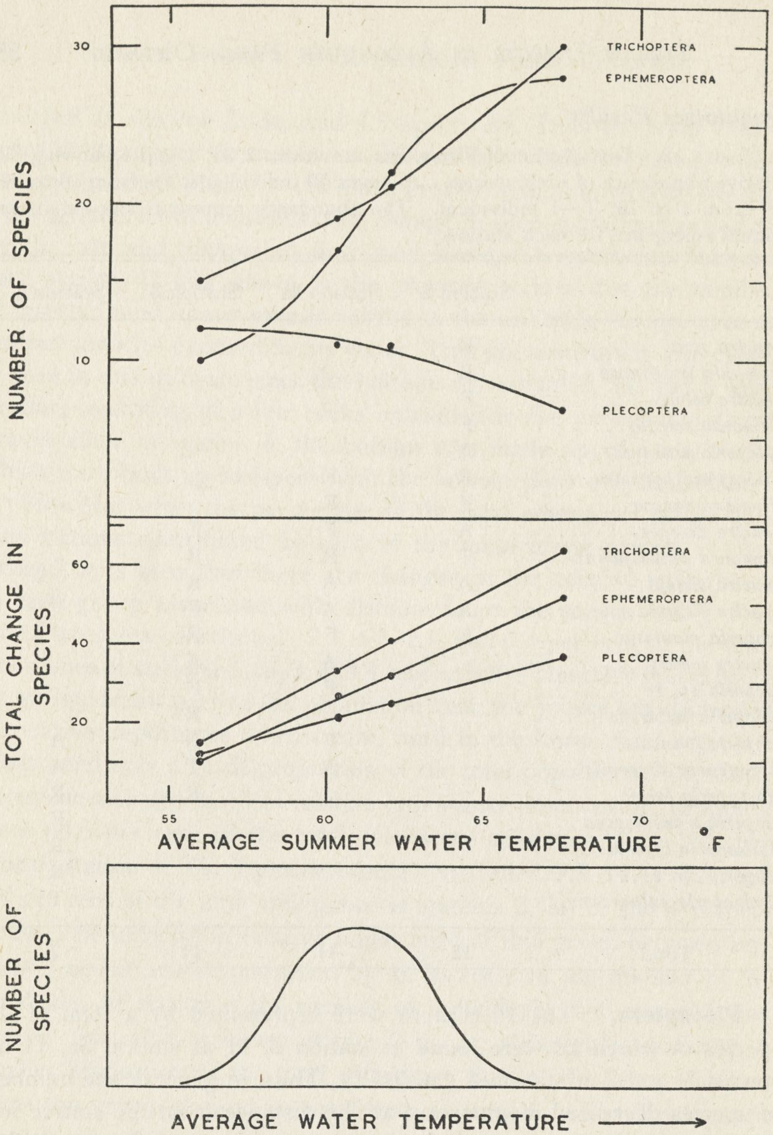

FIG. 8. Relationship of numbers of species of insects and temperature of the water.

Top panel: the relationship between number of species and average summer water temperature.

Centre panel: the relationship between the total change in species and the average summer water temperature.

Bottom panel: the hypothetical relationship between the number of species and average water temperature for any insect group over its complete temperature range in a stream.

There were no species common to stations 2 and 4 which were located at the upper and lower limits of this stream investigation. The faunas at the intermediate stations, 3a and 3, were similar and consisted of some species found at station 2 and others found at station 4, illustrating the progressive change that occurred downstream and the close faunal relationship existing between these two stations.

The change in the fauna downstream resulted from the successive disappearance of species found at the upper stations and addition of species found at the lower stations. The net decrease in the number of species resulted from the more rapid loss of upper-station species than gain of lower-station species (figure 8, top panel). It was found that there was a direct proportionality between the total change of species at successive stations and the average summer water temperature (figure 8, middle panel). There were 5 species found at station 2 which did not occur at station 3a while there were 4 species at the latter station which did not occur at station 2. Thus there was a total change of 9 species between these stations and an average temperature difference of 4.4 degrees Fahrenheit. The fauna at station 3 differed from that at station 3a by a total of 4 species, which included 2 eliminated and 2 added species, and the temperature index differed by 1.7 degrees. Eight species found at station 3 were eliminated at station 4 and there were 4 species at station 4 not found at station 3. This total change of 12 species was associated with an average temperature difference of 5.4 degrees Fahrenheit.

When the number of species belonging to each family occurring at a station was represented as a percentage of the total number of species found there, it was found that in general the Capniidae, Leuc-

Table 13.—Relative importance of the families of Plecoptera at the stations. The number of species in each family is represented as a percentage of the total number of species found at a station.

	Station 2	Station 3a	Station 3	Station 4
Capniidae	8.3%	9.1%		
Leuctridae	41.7%	36.4%	36.4%	
Nemouridae	33.3%	18.2%	9.1%	
Chloroperlidae	16.7%	27.3%	45.5%	57.1%
Perlidae		9.1%	9.1%	28.6%
Perlodidae				14.3%

tridae and Nemouridae decreased in relative importance downstream and the Chloroperlidae, Perlidae and Perlodidae increased (table 13). Consideration of the distribution of families at the stations augmented the information obtained from consideration of the distribution of species alone. Thus, although there were no species common to all the stations, one family, the Chloroperlidae, was represented at all the stations and increased in relative importance downstream, since it comprised 16.7 per cent of the population at station 2 and increased to 27.3, 45.5, and 57.1 per cent at stations 3a, 3, and 4 respectively.

When the relative abundance of each species at a station was compared along with the general distribution of species at the stations, it was found that the number of individuals decreased as the species approached the limits of its distribution (table 12). The species found at station 2 in almost every case showed their maximum abundance there and decreased numerically at stations farther downstream, having dropped out completely at station 4. The species found only at station 2 have a narrow range of thermal tolerance when considered from the standpoint of the stations used in this investigation, but it is probable that these would extend farther upstream if their complete distribution were known. The species common to station 4 and stations farther upstream showed a fairly wide range of tolerance, but in general the numbers were reduced at the upper stations, showing that the optimum conditions for the species prevailed at station 4. The species found only at station 4 would be those most likely to extend their distribution farther downstream.

Along with this numerical reduction it was found that the period of emergence for the species was restricted at the limits of its distribution. Those that were eliminated downstream were confined to a short period in the early part of the season at the lower stations, while at the upper stations the emergence occurred later in the season and in general extended for a longer period. For example, in 1940, *Leuctra sibleyi* emerged from June 4 to June 18 at station 2 and from May 31 to June 5 at station 3a. In 1941, this species emerged from May 21 to June 16 at station 2 and from May 16 to May 24 at station 3a. The species that were eliminated upstream from station 4 began to emerge on approximately the same date at the upper and lower stations but the period of emergence was reduced at the upper stations in general. This condition probably resulted from the slower fall cooling and spring warming of the water at station 4 compared with that at station 3 and 3a, and the higher maximum temperatures attained during the summer at the upper stations.

It was found that the period of emergence of Plecoptera at station 4 was restricted to the early summer, from late May to the middle of July, while at stations 2, 3a and 3 the emergence period extended from early spring to late fall. The late summer emergence at the upper stations resulted from the presence of *Leuctra tenuis* and *Leuctra decepta.* These were absent from station 4 as were also the early spring species including *Leuctra biloba* and the Capniidae.

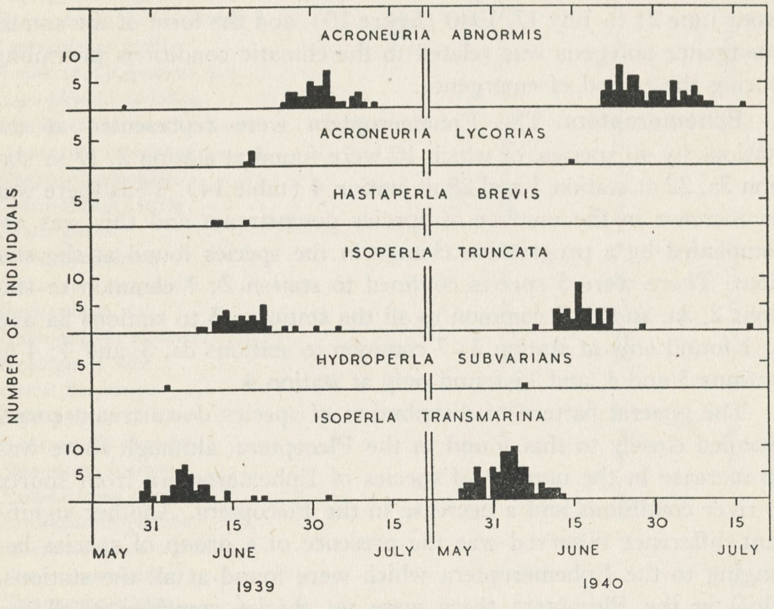

Fig. 9. Seasonal distribution of the emergence of representative Plecoptera at station 4 in 1939 and 1940.

The appearance of the species at a given station followed the same order each year. At station 4 the first species to appear each year was *Isoperla transmarina,* which was followed by *Hydroperla subvarians, Isoperla truncata, Hastaperla brevis, Acroneuria lycorias* and *Acroneuria abnormis* (figure 9). The species at the other stations also followed an orderly seasonal appearance each year. The date of first emergence, length of the emergence period and form of the emergence polygon of any species was subject, however, to annual variation. This seems to depend on the water temperature during the fall and spring preceding the emergence. Thus a warm spring pushed the date of the first emergence of a species forward and if the warm spell continued the period of emergence was short and the number of individuals emerging each day, large. Conversely, a cool spring delayed the date of first emergence, lengthened the period of emergence, and decreased the number of individuals that emerged each day. For example, *Acroneuria abnormis* at station 4 emerged from June 19 to July 11 in 1938, from June 25 to July 12, 1939 (figure 9), and from June 21 to July 17, 1940 (figure 10), and the form of the annual emergence polygons was related to the climatic conditions prevailing during the period of emergence.

Ephemeroptera. The Ephemeroptera were represented at the stations by 40 species, of which 10 were found at station 2, 17 at station 3a, 22 at station 3 and 28 at station 4 (table 14). Thus there was an increase in the number of species downstream and this was accompanied by a progressive change in the species found at the stations. There were 5 species confined to station 2; 1 common to stations 2, 3a, and 3; 4 common to all the stations; 5 to stations 3a and 3; 1 found only at station 3; 7 common to stations 3a, 3, and 4; 4 to stations 3 and 4, and 13 found only at station 4.

The general pattern of distribution of species downstream corresponded closely to that found in the Plecoptera, although there was an increase in the number of species of Ephemeroptera from source to river conditions and a decrease in the Plecoptera. Another significant difference observed was the presence of a group of species belonging to the Ephemeroptera which were found at all the stations, while in the Plecoptera there were no species common to all the stations. The faunas at stations 2 and 4, which were at the upper and lower limits of the investigation, differed markedly while those at stations 3 and 3a were similar.

The progressive change in the fauna downstream resulted from the disappearance of species found at the upper stations and the addition of species found at lower stations. The net increase downstream resulted from a more rapid gain than loss of species (figure 8, top

TABLE 14.—Distribution of Ephemeroptera at stations 2, 3a, 3, and 4, showing the relative abundance of each species. A—over 50 individuals; F—from 10 to 50; R—from 1 to 10; T—1 individual. The abundance represents the maximum annual emergence for each station.

	Station 2	Station 3a	Station 3	Station 4
Centroptilum convexum	T			
Centroptilum semirufum	R			
Ameletus ludens	F			
Stenonema carolina	A			
Baetis brunneicolor	A			
Leptophlebia debilis	A	A	A	
Heptagenia pulla	F	A	A	F
Ephemerella sp. (*bicolor* gr.)	F	R	R	F
Leptophlebia mollis	T	F	A	F
Baetis sp. (*pygmaeus* gr.)	T	F	A	A
Leptophlebia adoptiva		F	F	
Stenonema rubromaculatum		F	F	
Stenonema ?vicarium		R	R	
Epeorus humeralis		F	R	
Centroptilum simile		R	T	
Baetis parvus			T	
Baetis cingulatus		F	F	R
Stenonema canadense		F	F	F
Baetis pluto		F	A	F
Habrophlebia vibrans		A	A	T
Heptagenia hebe		R	R	T
Baetis flavistriga		A	A	A
Leptophlebia volitans		T	F	A
Ephemerella invaria			T	F
Stenonema fuscum			F	F
Pseudocloeon carolina			R	F
Leptophlebia guttata			R	T
Stenonema heterotarsali				F
Stenonema rubrum				A
Stenonema luteum				R
Isonychia bicolor				A
Heterocloeon curiosum				A
Heptagenia ?minerva				R
Ephemerella sp. (near *serrata*)				R
Pseudocloeon cingulatum				F
Baetis vagans				F
Stenonema sp. (near *integrum*)				F
Ephemerella subvaria				T
Pseudocloeon ?dubium				F
Pseudocloeon ?virile				R
Total	10	17	22	28

panel). When the total change of species at successive stations was determined it was found that this change was directly related to the average summer water temperature (figure 8, centre panel).

Consideration of the relative abundance of a species at different stations indicates where optimum conditions for that species occur within the limits of this investigation. For example, *Leptophlebia volitans* was represented abundantly at station 4, frequently at station 3, by a trace at station 3a and was absent from station 2 (table 14). Thus, as was found in the Plecoptera, the number of individuals decreased as the limits of distribution of a species were approached. The species found only at station 2 would probably extend their distribution farther upstream while those confined to station 4 would most likely be found in lower sections of the stream. Further, the species that were eliminated downstream emerged earlier each year and had a shorter emergence period at the lower stations than at the upper sta-

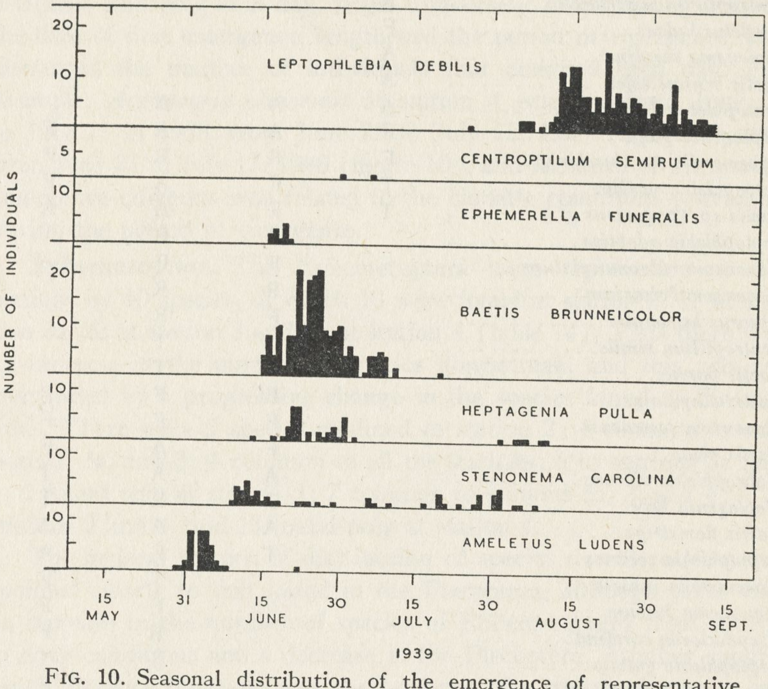

FIG. 10. Seasonal distribution of the emergence of representative Ephemeroptera at station 2 in 1939.

tions, as was found to be the case in the Plecoptera; the species that were eliminated upstream also had a restricted emergence at the limit of their distribution.

The seasonal distribution of Ephemeroptera showed the same general sequence as was found in the Plecoptera. The species found at any one station appeared in the same general order each year, with some confined to the early season, others to midsummer, others to the late summer, while some emerged throughout the summer months (figure 10). There were no species that emerged as early in the spring as the first Plecoptera species at any station and the emergence continued later in the fall than did that of the Plecoptera.

The date of first emergence and the nature of the emergence polygon of any species varied from year to year and these variations seemed to be directly related to the seasonal water temperature at the station. For example *Ameletus ludens* at station 2 began to emerge on May 29, 1939, and had completed its emergence by June 8 with the exception of one individual which emerged on June 22 (figure 10). Thus the emergence period lasted for 25 days although all but one individual had emerged in 11 days. In 1940 this species began to emerge 5 days later, June 2, and continued until June 27, a period of 26 days, but in this year the emergence was more evenly distributed throughout the period. Associated with this change was a period of high temperature from May 28 to June 2, 1939, following which the temperature dropped, while in 1940 comparable temperatures were not reached until June 2 and 3, following which the temperature dropped.Thus it is probable that the high temperatures attained in 1939 were responsible for the earlier appearance of this species that year as well as for the shortened period of emergence.

Such a period of high temperature does not affect noticeably the date of first emergence of species that appear later in the summer. Thus *Baetis brunneicolor* began to emerge on June 15, 1939, at station 2, while in 1940 it first emerged on June 12, four days earlier. The apparent lack of correlation between the first emergence dates of these two species in 1938 and 1939 probably resulted from the water temperatures effective between the dates of their initial emergence. Miller (1941) proposed that the time required for lake water of different depths to acquire a certain accumulated heat in day-degrees explained the varying time of emergence of Chironomidae at these depths. It is probable that a similar explanation would account for the annual variation in time of emergence of stream insects as well.

Trichoptera. The Trichoptera were represented at the stations by a total of 46 species of which there were 15, 19, 21, and 30 found respectively at stations 2, 3a, 3, and 4 (table 15). Thus there was an increase in the number of species downstream as was found in the Ephemeroptera. There were 7 species confined to station 2; 2 common to stations 2 and 3a; 4 to stations 2, 3a, and 3; 2 to stations 2, 3a, 3, and 4; 3 common to stations 3a and 3; 7 to stations 3a, 3, and 4; 1 to stations 3a and 4; 5 to stations 3 and 4; and 15 found only at station 4.

The changes in the fauna downstream resulted from the elimination of species found in the upper reaches of the stream and the addition of species found in the lower reaches. The net increase in number of species found downstream resulted from a more rapid rate of gain than loss of species (figure 8, top panel). The total change of species at successive stations was determined by summing the number eliminated from the nearest upstream station and the number added, and it was found that this change was proportional to the average summer water temperature (figure 8, centre panel).

As was found in the distribution of Plecoptera and Ephemeroptera, the number of individuals of any species decreased in general as the limits of distribution of the species were approached. For example, *Lepidostoma grisea* occurred abundantly at station 2, rarely at station 3a, while only a single individual emerged at station 3 (table 15). The species found only at station 2, which had the lowest average temperature of any of the stations used in this investigation, showed a narrow range of temperature tolerance and may be described as stenothermal cold-tolerant forms. However, if the complete distribution of such species were known, it is probable that they would show a greater range and would extend farther upstream. Similarly the species found only at station 4, which was located at the other extreme of temperature within the limits of this study, may be termed stenothermal warmth-tolerant species, but would likely extend farther downstream if their complete distribution were known. The species that emerged from two or more stations showed various ranges of thermal tolerance and *Psychomyia diversa* and *Polycen-*

Table 15.—Distribution of Trichoptera at stations 2, 3a, 3, and 4, showing the relative abundance of each species. A—over 50 individuals; F—from 10 to 50; R—from 1 to 10; T—1 individual. The abundance represents the maximum annual emergence for each station.

	Station 2	Station 3a	Station 3	Station 4
Hydroptila sp.	R			
Dolophilus moestus	F			
Parapsyche apicalis	F			
Goera stylata	F			
Micrasema sprulesi	F			
Rhyacophila vibox	F			
Lepidostoma ontario	A			
Hydropsyche ventura	F	F		
Neophylax autumnus	R	R		
Philopotamus distinctus	A	A	F	
Rhyacophila carolina	F	F	R	
Stenophylax guttifer	T	R	T	
Lepidostoma grisea	A	R	T	
Psychomyia diversa	R	R	R	R
Polycentropus confusus	R	R	F	A
Cheumatopsyche pettiti		F	F	
Agapetus sp.		R	R	
Hydropsyche betteni		F	F	
Chimarrha aterrima		F	A	A
Nyctiophylax vestitus		F	R	F
Plectrocnemia cinerea		R	R	A
Athripsodes dilutus		T	R	F
Rhyacophilo fuscula		R	R	F
Hydropsyche sparna		R	F	R
Athripsodes angustus		T	R	F
Mystacides sepulchralis		R		T
Osythira sp.			T	T
Agraylea costello			T	F
Phylocentropus placidus			T	R
Cheumatopsyche campyla			R	A
Psychomyella flavida			R	R
Rhyacophila vuphipes				R
Chimarrha socia				R
Chimarrha lucia				A
Hydropsyche morosa				A
Hydropsyche dicantha				A
Hydropsyche recurvata				A
Athripsodes alces				F
Athripsodes wetzeli				R
Oecetis avara				R
Macronema zebratum				A
Neureclipsis crepuscularis				A
Neureclipsis parvulus				F
Micrasema wataga				F
Cheumatopsyche gracilis				A
Cheumatopsyche miniscula				A
Total	15	19	21	30

tropus confusus, which occurred at all the stations, may be described as eurythermal species.

The emergence periods of different species were seasonally distributed throughout the summer months from early May on through September at all stations. The first species to emerge at station 4 each year appeared later than those at the upper stations and this seemed to result from the slower rise in water temperature at this station dependent on the greater volume of water to be heated in the spring. The species emerged in the same order each year, and the date of first emergence and length of the emergence period were affected by annual temperature variations as was found for species of Plecoptera and Ephemeroptera. The emergence polygons of a few representative species of Trichoptera have been illustrated in figure 11.

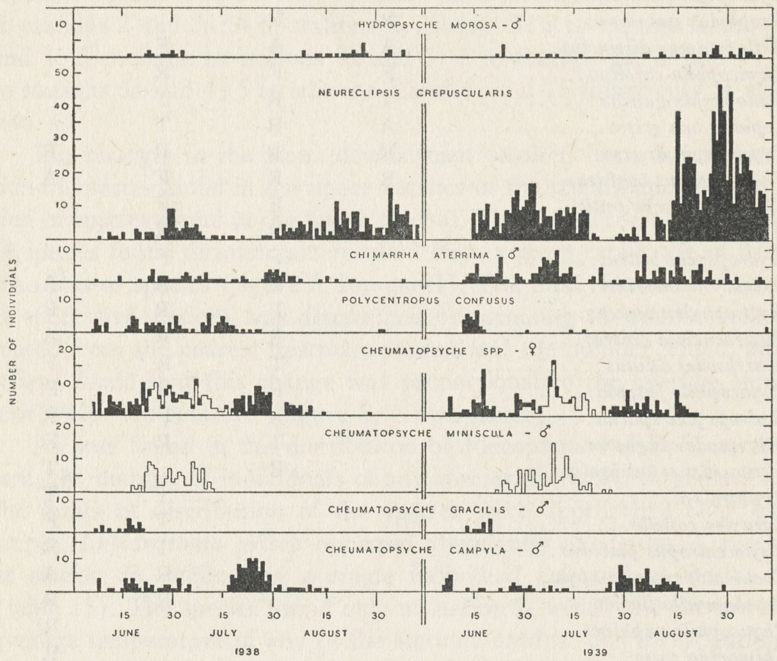

FIG. 11. Seasonal distribution of the emergence of representative species of Trichoptera at station 4 in 1938 and 1939.

An indication of the emergence of two generations during the summer at station 4 was obtained for certain species including *Hydropsyche morosa* and *Cheumatopsyche campyla* (figure 11). Marshall (1939) found two brood flights of some species of Trichoptera in the lake Erie region including *Cheumatopsyche campyla* and suggests the possibility that the individuals of the second brood are the descendants of those of the first, making two generations in one season. Detailed study of the development of the immature stages is necessary before a definite statement regarding second generations may be made. However, no consistent suggestion of two seasonally isolated groups in any species was obtained at the other stations and it is probable that second generations do occur in certain species at station 4 where a high average summer temperature is maintained for a long period. Miller (1941) found evidence of the occurrence of two generations of certain species of Chironomidae in shallow lake water and pointed out that certain species with only one generation a year in northern waters were known to have two generations in their southern range where the summer is longer. He associated the occurrence of two generations with the day-degree requirements for development of the species and it seems probable, from the results obtained for some species at station 4, that a similar explanation would account for the appearance of two seasonally isolated groups within a species in stream environments with a prolonged period of high average summer temperature.

Discussion

The results of this investigation showed that there is a differential linear distribution of insects in rocky riffle sections of a stream which is related to the distance from the source. Associated with this distribution is the increase in the size of a stream as it develops from the source and an increase in the average water temperature. It has been shown that temperature is of prime importance in limiting the linear distribution of species and it is probable that the other factors are of secondary importance in this respect.

A direct correlation was found between the total change of species at successive stations and the average summer water temperatures found there. This total change was derived by summing the number of species eliminated and number of species added at each station. The elimination of species downstream probably resulted from the increase in water temperature. It was found from a series of experiments on the nymphs of Plecoptera that although the lethal temperature was well above the temperatures obtaining in the stream, the value was lower for the species found at the upper stations than for those found at the lower stations. Within this group the species show a gradation of upper limits of temperature tolerance. It would appear from these results that the nymphs are able to withstand the highest stream temperatures, at least for a short period, but prolonged exposure to these may limit the distribution of certain species. Since the experiments were carried out on practically full-grown nymphs in every instance, the possibility that the limiting effect of high temperatures may be active on some other stage of the life-cycle cannot be overlooked. Ide (1935) studied the effect of temperature on the distribution of Ephemeroptera in a stream and found that species dropped out downstream became successively limited to the early season at the lower stations, he states "that the latest date at which individuals emerge successfully at a station is determined by the temperatures obtaining at that station." He proposed that this resulted from a process of selection on the nymphs by heat over a number of years. This explanation could well account for the elimination of species downstream found in the present study, since it has been shown that the number of individuals in a species decreased as the species approached the lower limit of its distribution, and evidence of the restriction of the emergence period to the early part of the season as the species approached its lower limit was obtained.

The absence of certain species from the upper stations seemed to result from the lower average temperatures found there, which may retard the rate of growth sufficiently to prevent the species from completing their life-cycle. It has been shown that the temperatures prevailing prior to emergence affect the date of first emergence of a species at a station from year to year so that, if the average temperature differences at two stations were great enough, it is probable that this would limit the distribution as Ide (1935) found to be the case in the distribution of Ephemeroptera in a stream. Since the maximum temperatures recorded at stations 3 and 3a were higher than those recorded at station 4, although the latter was farther downstream, it is possible that certain species found at the lower station were eliminated at stations 3 and 3a by the higher temperatures which may have proved lethal.

Since there were no species of Plecoptera common to stations 2 and 4, located at the extremes of average summer water temperatures found in this investigation, it would seem that the average range of thermal tolerance of this group was small. On further analysis it was found that 45.5 per cent of the species had a range of thermal tolerance extending from either station 2 or station 4 to the intermediate stations 3 and 3a, and 54.5 per cent had a range restricted to one section of the stream. The Ephemeroptera had only 40.0 per cent of the species with a wide range of thermal tolerance, and 60.0 per cent with a restricted range, although there were some species common to all the stations and thus able to withstand the widest temperature extremes obtained. The average range of thermal tolerance of the species of Trichoptera was practically identical with that of the Plecoptera with 45.6 per cent of the species showing a wide range and 54.4 per cent a narrow range.

In all the groups the species that were confined to the upper station are probably stenothermal cold-tolerant forms while those found at the lower station only are stenothermal warm-tolerant species. The species of Ephemeroptera and Trichoptera that were found at all the stations seem to be eurythermal but there were no species of Plecoptera that could be classified in this manner.

Since there was a decrease in the number of species of Plecoptera found downstream it would seem that this group is made up primarily of species adapted as cold-tolerant. This is substantiated by distribution records of the group and the occurrence of winter Plecoptera which complete their life-cycle during the winter with the adults living on the snow and ice at the margins of streams (Frison, 1929). The number of species in the Ephemeroptera and Trichoptera increased downstream; in general it seems, therefore, that these groups are made up primarily of warmer water species. Since the rate of increase of species was decreasing at station 4 in the Ephemeroptera and still increasing in the Trichoptera, it would seem that in the latter group there were more species adapted to warm water conditions, and these to warmer water in general, than was the case in the Ephemeroptera.

Within the temperature limits of the present investigation the observed distribution suggests that species of each group, provided the temperature range were extended, would exhibit a normal curve of distribution along the temperature gradient. The positions of the mode and the length of the distribution diagram would depend on the average optimal temperature and the range of thermal tolerance. The height of the mode would vary also, dependent on the number of species belonging to any insect group. For the perfect expression of these curves, environmental conditions other than those dependent on temperature would have to be uniform. The number of species of Plecoptera decreased downstream as the average temperature increased, while the Ephemeroptera and Trichoptera increased (figure 8, top panel). The nature of the respective increases in the last two groups differed however, since between stations 3 and 4 the rate of increase slowed down in the Ephemeroptera while it continued unabated in the Trichoptera. Thus, considering these distributions in the light of the hypothetical distribution outlined above, the portion of the Plecoptera distribution diagram obtained in this study was a section to the right of the mode and it would seem probable that the mode would occur at a temperature close to that of station 2. The diagram for the Ephemeroptera distribution consisted of a section immediately to the left of the mode and the mode would occur at a temperature close to that found at station 4. The Trichoptera distribution also is illustrated by a section of the hypothetical distribution curve to the left of the mode but no indication of the position of the mode was obtained and it may be assumed that it would occur farther downstream where a higher average temperature prevailed.

Further insight into the role played by temperature in limiting the distribution of insect species in a stream can be obtained from a consideration of the fauna at station 1. There was an intermittent flow at this station and although it was located closer to the source than station 2, the average summer temperature approximated that found at stations 3a and 3. Two species of Trichoptera. *Hydropsyche bettini* and *Cheumatopsyche pettiti,* were found at stations 1, 3a, and 3, but were not found at station 2. Ide (1935) also gives an example of such a station not falling into the direct series. Thus this distribution indicates that temperature sets limits to the distribution of insects and that species are found in widely separated sections of a stream providing the prevailing water temperatures are within the limits required for development of the species.

The results showed that the total number of insects emerging from one type of bottom at different levels of the stream gradient is not related as closely to temperature as is the number of species. The evidence obtained suggested that the total number of insects is more closely related to the utilizable surface area of bottom particles exposed to the water. However these results are not entirely in agreement with findings elsewhere. Needham (1928) and Pate (1931, 1932, and 1933) showed a relationship between the amount of bottom fauna in a stream and the width. They found that in general small headwater streams are more productive per unit area than the large streams. However it is probable that the stream conditions are much different in the various areas studied by other investigators. In the light of more recent investigation Needham has found that certain large rivers such as the Klamath river in northern California are very rich in the amount of bottom fauna present and that a high organic content was associated with this condition. Further, he states (Needham, 1938) that "It has become quite evident that what is true for one drainage area does not by any means hold true for another· Each presents its own environmental peculiarities and each must be studied individually."

SUMMARY

1. An investigation of the quantitative and qualitative distribution of insects in streams of Algonquin Park, Ontario, was carried out to determine the effect of different environmental conditions on the distribution of insects.

2. The cage-trap method which samples the emergence of insects from unit areas was used in the study since it is applicable to the diverse habitats associated with lotic environments.

3. Data were obtained from ten stations selected throughout the Madawaska river system.

4. It was found that when hourly collections were made from a cage-trap the value obtained for the total *number* of insects which emerged in a twenty-four interval was approximately twice that obtained when only one collection was made in the same interval.

5. In general any one species emerged at the same time each day and different species emerged at different hours throughout a twenty-

four-hour interval. It was found that the maximum total emergence from a rocky riffle in midsummer occurred at 11.00 p.m. each day and that the majority of insects emerged between sundown and midnight.

6. The insect population was reduced in areas where the bottom was scoured by a severe freshet. The reduction resulted from the loss of individuals which were dislodged and swept downstream by the current and the elimination of others through molar action. The effect of the freshet was minimized in areas where the bottom was relatively stable and consisted of large particles which afforded shelter.

7. An intermittent flow and consequent drying of the stream bed limited the number of individuals and species present. It was found that species of fixed habit, such as certain of the Trichoptera and the Simuliidae, were eliminated rapidly as the water receded from the stream margins, while the free-roving forms such as nymphs of Ephemeroptera were able to follow the receding water and thus were not affected by the desiccation in its early stages.

8. The transformation of a shallow rocky rapids into a deep sedimented pool by a beaver dam brought about an immediate reduction in the number of individuals and number of species in the area. The decrease resulted from the elimination of a large group of insects that were dependent on current for respiration and feeding, and the addition of a smaller group of quiet-water species which extended their distribution into the area once the restrictions of current were removed. A small number of species showed a wide range of habitat tolerance and persisted under both sets of conditions.

9. A variation in the number of species and number of individuals was found associated with different types of bottom in a restricted section of the stream. Rocky riffles were most productive, followed in order by gravel, muck, and sand bottoms. The diversity of the fauna found on any particular type of bottom was related to the variety of utilizable microhabitats associated with the bottom type. It has been suggested that the number of insects present in any area is related to the habitable surface area of bottom particles exposed to the water.

10. A change was found in the species composing the fauna of rapid riffles at different distances from the source of the stream. This change resulted from the progressive elimination of species found in

the upper reaches of the stream and the addition of species found in the lower reaches. A direct correlation was found between the total change in the number of species in successive riffles at different distances from the source and the average summer water temperature.

11. The emergence periods of different species were seasonally segregated as a result of differences in thermal requirements and the species emerged in the same order each year. The date of first emergence, length of the emergence period and form of the emergence histogram of any species differed annually probably in response to differences in the water temperatures during the developmental period from oviposition to emergence.

12. Species were found in widely separated sections of the stream providing the temperatures in these areas were suitable for the development of the species.

13. The quantitative and qualitative distribution of insects observed in streams results from the complex interaction of many environmental factors, of which temperature, nature and configuration of the bottom particles, and rate of flow are of fundamental importance.

LIST OF SPECIES

The following species belonging to the orders Plecoptera, Ephemeroptera and Trichoptera were identified from the collections made during the investigation.

PLECOPTERA

Classification after Frison (1935).

Nemouridae

Nemoura punctipennis Claassen
Nemoura serrata Claassen
Nemoura trispinosa Claassen
Nemoura venosa Banks

Leuctridae

Leuctra biloba Claassen
Leuctra decepta Claassen
Leuctra duplicata Claassen
Leuctra hamula Claassen
Leuctra sara Claassen
Leuctra sibleyi Claassen
Leuctra tenuis Pictet

Capniidae

Capnia sp.
Allocapnia pygmaea (Burm.)

Perlidae

Acroneuria abnormis (Newman)
Acroneuria lycorias (Newman)

Perlodidae

Hydroperla subvarians (Banks)

Chloroperlidae

Hastaperla brevis (Banks)
Isoperla montana Banks
Isoperla sp. 1
Isoperla sp. 2
Isoperla transmarina (Newman)
Isoperla truncata Frison
Alloperla imbecilla (Say)
Alloperla mediana Banks

EPHEMEROPTERA

Classification modified from Needham, Traver and Hsu (1935).

Heptageniidae

Stenonema canadense Walker
Stenonema carolina Banks
Stenonema fuscum Clemens
Stenonema heterotarsale McDunnough
Stenonema luteum Clemens
Stenonema rubromaculatum Clemens
Stenonema rubrum McDunnough
Stenonema sp. (near *integrum* McDunnough)
Stenonema ?vicarium Walker
Heptagenia hebe McDunnough
Heptagenia ?minerva McDunnough
Heptagenia pulla Clemens
Epeorus humeralis Morgan
Arthroplea bipunctata McDunnough

Baetidae

Metretopinae
  Siphloplecton basale Walker

Siphlonurinae
  Ameletus ludens Needham
  Siphlonurus alternatus Say
  Siphlonurus quebecensis Provancher
  Isonychia bicolor Walker

Leptophlebiinae
  Leptophlebia johnsoni McDunnough
  Leptophlebia adoptiva McDunnough
  Leptophlebia debilis Walker
  Leptophlebia guttata McDunnough
  Leptophlebia mollis Eaton
  Leptophlebia volitans McDunnough
  Blasturus cupidus Say
  Blasturus nebulosus Walker
  Choroterpes basalis Banks
  Habrophlebia vibrans Needham

Baetiscinae
  Baetisca laurentina McDunnough

Ephemerellinae
  Ephemerella deficiens Morgan
  Ephemerella funeralis McDunnough
  Ephemerella invaria Walker
  Ephemerella lutulenta Clemens
  Ephemerella sp. (near *bicolor* Clemens)
  Ephemerella sp. (near *serrata* Morgan)
  Ephemerella subvaria McDunnough

Caeninae
  Tricorythodes sp.
  Brachycercus sp.
  Caenis sp.

Baetinae

Baetis brunneicolor McDunnough
Baetis cingulatus McDunnough
Baetis flavistriga McDunnough
Baetis ?frondalis McDunnough
Baetis parvus Dodds
Baetis pluto McDunnough
Baetis sp. (near *pygmaeus* Hagen)
Baetis vagans McDunnough
Centroptilum convexum Ide
Centroptilum ?ozburni McDunnough
Centroptilum semirufum McDunnough
Centroptilum simile McDunnough
Heterocloeon curiosum McDunnough
Pseudocloeon carolina Banks
Pseudocloeon cingulatum McDunnough
Pseudocloeon ?dubium Walsh
Pseudocloeon ?virile McDunnough
Cloeon minor McDunnough
Cloeon rubropictum McDunnough
Cloeon simplex McDunnough
Cloeon triangulifer McDunnough

TRICHOPTERA

Classification modified form Betten (1934)

Rhyacophilidae

Rhyacophilanae

Rhyacophila carolina Banks
Rhyacophila fuscula (Walker)
Rhyacophila invaria Walker
Rhyacophila vibox Milne
Rhyacophila vuphipes Milne

Glossosomatinae

Agapetus sp.

Hydroptilidae

Agraylea costello Ross
Hydroptila sp.
Oxyethira sp.

Philopotamidae

Philopotamus distinctus Walker
Dolophilus moestus (Banks)
Chimarrha aterrima Hagen
Chimarrha lucia Betten
Chimarrha socia Hagen

Hydropsychidae

Hydropsychinae

Parapsyche apicalis (Banks)
Diplectrona modesta Banks
Hydropsyche betteni Ross
Hydropsyche dicantha Ross
Hydropsyche morosa (Hagen)
Hydropsyche recurvata Banks
Hydropsyche sp.
Hydropsyche sparna Ross
Hydropsyche ventura Ross
Cheumatopsyche campyla Ross
Cheumatopsyche gracilis (Banks)
Cheumatopsyche miniscula (Banks)
Cheumatopsyche pettiti (Banks)

Macronematinae

Macronema zebratum Hagen

Polycentropidae

Polycentropinae

Neureclipsis crepuscularis (Walker)
Neureclipsis parvulus Banks
Phylocentropus placidus (Banks)
Plectrocnema cinerea (Hagen)
Polycentropus confusus Hagen
Polycentropus maculatus Banks
Polycentropus pentus Ross
Nyctiophylax vestitus (Hagen)

Psychomyidae

Psychomyia diversa Banks
Psychomyella flavida (Hagen)

Molannidae

Molanninae

Molanna sp.

Leptoceridae

Leptocerinae

Athripsodes alces Ross
Athripsodes angustus (Banks)
Athripsodes dilutus (Hagen)
Athripsodes wetzeli Ross
Oecetis avara (Banks)
Oecetis inconspicua (Walker)
Mystacides sepulchralis (Walker)

Limnephilidae

Limnephilus consocius Walker
Stenophylax guttifer (Walker)
Platycentropus indicans (Walker)
Neophylax autumnus Vorhies
Pycnopsyche aglonus Ross

Sericostomatidae

Brachycentrinae

Micrasema sprulesi Ross
Micrasema wataga Ross

Goerinae

Goera stylata Ross

Lepidostomatinae

Lepidostoma costalis (Banks)
Lepidostoma grisea Banks
Lepidostoma ontario Ross

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