AN INVESTIGATION OF THE SUCCESS OF RAINBOW TROUT POPULATIONS IN TEN LAKES RELATIVE TO LIMITING ENVIRONMENTAL FACTORS

Thesis for the Degree of Ph. D.

MICHIGAN STATE UNIVERSITY

Wayne H. Tody

1964

This is to certify that the

thesis entitled

An investigation of the success of
rainbow trout populations in ten
lakes relative to limiting
environmental factors

presented by

Wayne H. Tody

has been accepted towards fulfillment
of the requirements for

Ph. D. degree in Fisheries and Wildlife

E. W. Roelofs
Major professor

Date February 25, 1964

O-169

ABSTRACT

AN INVESTIGATION OF THE SUCCESS OF RAINBOW TROUT POPULATIONS IN TEN LAKES RELATIVE TO LIMITING ENVIRONMENTAL FACTORS

by Wayne H. Tody

The data presented are from a study directed to the determination of the influence of environmental factors on the success of artificially established rainbow trout populations in warm-water lakes. The interaction of growth and mortality is analyzed relative to the efficiency of each population in producing an available stock of trout for the angler.

Ten small lakes near the 70 F isotherm in central Michigan were selected as the site for the study. Field investigations were conducted in 1959, 1960 and 1961. Trout were planted in April and May following rotenone treatment the preceding season. Throughout the ice-free season data were collected on trout growth, food habits, and sources of mortality. The lakes were studied simultaneously with regard to physical, chemical, and biological characteristics. In October the remaining trout were removed for estimation of weight and numbers.

It was found that the relative biomass of fish present was the dominant environmental factor influencing trout growth. The effect of competition from non-trout fish species was especially effective in delimiting trout growth. It was found that the progeny from a few pairs of adult bluegills caused a nearly complete cessation of trout growth within a few weeks after the hatch of bluegills. Secondarily the relative areas of the littoral zone was of importance in determining growth. The trout inhabited the shallow littoral areas of the lakes throughout the season and fed principally on benthic organisms.

All available evidence pointed to predation as the dominant source of natural mortality. Loons and northern pike were associated with heavy losses of trout in two of the lakes. Natural mortality was found to have somewhat more influence than growth on the efficiency of the populations in providing a large standing crop of trout for the angler.

On the basis of the experience of this study and a review of the literature it was concluded that rainbow trout can be successfully managed in lakes where competition from non-trout species is controlled if maximum water temperatures do not exceed 78 F in the well-oxygenated zone. In lakes where temperature is relied upon to control competition of other fish species to favor trout maximum temperatures should not exceed 65 F.

Frontispiece. Marl Lake

AN INVESTIGATION OF THE SUCCESS OF RAINBOW TROUT POPULATIONS IN TEN LAKES RELATIVE TO LIMITING ENVIRONMENTAL FACTORS

by

Wayne H. Tody

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Fisheries and Wildlife

1964

ACKNOWLEDGMENTS

I am grateful for the support and facilities provided by the Fish Division, Michigan Department of Conservation, through the offices of Dr. J. W. Leonard, Mr. F. A. Westerman, and Dr. G. P. Cooper in making this study possible. Many employees of the Department furnished assistance whenever it was needed. I am especially grateful to Mr. John Scott, Mr. Roger Wicklund, Mr. O. H. Clark, and the other members of the Lake and Stream Improvement Section for all of the assistance and patience so generously offered throughout the course of this study. I appreciate the help of Mr. Paul Earl who drafted the figures.

Special acknowledgment is due Dr. Eugene W. Roelofs, chairman of my doctoral committee, for his valuable guidance throughout the program and for his helpful suggestions on improvement of the manuscript. Dr. Paul Fromm, also of the doctoral committee, was a source of inspiration through his stimulating interest in the study.

I am indebted to Robert Carter, Larry Lewis, Alex Strange, and Sandy Sanderson the owners or custodians of the experimental lakes. Not only did they offer the utmost in cooperation and every possible assistance, it became a real pleasure to meet and work with them.

TABLE OF CONTENTS

Page

LIST OF TABLES

Table		Page

LIST OF FIGURES

Figure		Page

INTRODUCTION

This is a study of the relative success of rainbow trout stocked in ten lakes offering diverse environmental conditions. In a sense this is a study of production of artificially established rainbow trout populations. In a broader sense it is intended as an investigation of environmental factors in a lake which influence growth and mortality and thus determine success of the population.

The lakes selected for this study range from extremely shallow unstratified bodies of water to deep-basin lakes exhibiting marked thermal stratification. The ten lakes range in size from 3 to 23 acres. In other characteristics the lakes vary widely.

Trout were planted in April and May following rotenone treatments to eliminate the existing fish populations. In October the surviving trout were removed, measured in size, and estimated in numbers. Thus the trout were used to test the lake environment for only the ice-free season. Throughout the season, measurement was made of growth rates, and a detailed record was kept of all known mortality. The lakes were studied simultaneously with regard to physical, chemical and biological characteristics of the environment.

The dynamics of each population were computed for the season. It was found that the relative size of the littoral zone and relative population density were dominant environmental factors influencing the rate of growth. Circumstantial evidence pointed to predation as the dominant environmental factor influencing the rate of natural mortality. The interaction of rate of growth and rate of mortality are discussed quantitatively as the determinants of production. The efficiency of each population in utilizing the inherent productivity of the lake and providing a maximum trout stock to the angler are also discussed.

Lastly, a review of temperature as a limiting environmental factor is made from the literature and from the experience gained in this study.

Background

The rainbow trout is a popular game fish wherever it is found in nature, or can be successfully distributed from domestic hatchery sources to provide additional angling opportunity. A comprehensive review of stocking as a tool of trout management was made by Cooper (1959). The rainbow trout is often introduced into both lake and stream environments where it cannot be expected to spawn successfully, but where a satisfactory return to the angler will be realized before the stock is completely depleted. It has often been found that lake plantings contribute more to the angler catch both in numbers and weight than do stream plantings. This apparently is true because the lake offers a more favorable environment for both growth and survival than does the stream environment. However, the success of lake plantings varies tremendously. This is especially apparent when rainbow trout are planted in the warmer lakes, and in lakes with extensive populations of other fish species. It is generally held that trout cannot be expected to succeed in lakes unless at least 10 percent of the lake volume is of a temperature not over 70 F and contains at least 5.0 ppm of dissolved oxygen (Hubbs and Eschmeyer, 1939; Cooper, 1940; Mullan and Tompkins, 1959; many others). Physiological literature on the other hand (Brett, 1956) suggests that rainbow trout can live and grow successfully in waters that do not exceed 78 F for more than a few hours at any time throughout the warm-weather season. In even the shallow lakes north of the 70 F isotherm it would seem that this latter condition could often be met. In such lakes, containing some water less than 78 F with 5.0 ppm of dissolved oxygen at all times during the year, if rainbow trout could not survive and grow at nominal rates (compared to cold-water lakes) it would appear that environmental factors other than temperature must be responsible. It was in this sense that this study was established, to study not only temperature but other environmental factors that might limit trout success in warm-water lakes.

Several additional factors exist at present that stimulate interest in the possible success of rainbow trout in relatively warm-water lakes. Many of the small lakes in the north-central states do not furnish satisfactory fishing with their endemic population of centrarchids, bullheads, perch, and other fishes. Apparently these fish utilize the available food supply for reproduction and maintenance requirements with slow growth of the older individual fish. Consequently the fish are small and generally unattractive to the fisherman. The use of toxicants to eradicate these endemic species is rapidly gaining in popularity as a fish management tool. Many of the lakes where this management practice is desirable (especially privately owned lakes) have generally been considered too warm to support trout.

A further interest in the success of trout in relatively warm lakes comes about through the need for an interim species in chemical lake rehabilitation involving stunted panfish control and introduction of predatory game fish species. The purpose of the interim species is to provide fishing while the other game species reproduce and grow to catchable size. The rainbow trout grows rapidly, is acceptable to the angler at relatively small size and is easily reared in the hatchery; thus it seems ideally suited as an interim species provided that it can thrive in a relatively warm environment.[1]

---

[1]Since this study was initiated in 1959 the rainbow trout has been successfully used as an interim species in Michigan lakes following chemical treatment to control stunted panfish, based on the preliminary results of this study.

THE STUDY AREAS

Ten small, privately owned lakes representing diverse habitat conditions in the central area of the lower peninsula of Michigan were selected for this study. Lakes of small size were chosen to limit the requirements of hatchery trout and to facilitate field observation. The use of private lakes with restricted fishing enabled some control over population density, and provided creel census data through contract agreement with the landowner. The final lake selection was based on considerations of depth, stratification, and total alkalinity to provide a broad range of individual lake types.

The lakes are located near the center of the peninsula where temperatures vary about 25 F diurnally, but average between 68 and 70 F in July, the warmest month of the year in this area (Yearbook of Agriculture, 1941). The location of the ten lakes relative to the climatic isotherms is shown in Figure 2.

Six of the ten lakes in this study, namely, Doyle, Ryan, Little, Slide, Marl, and Little Headquarters lie in Roscommon County, on the club property of the Mid-Forest Lodge Association. This club, consisting of 400 members, owns 28 sections of land essentially in a square block. The area is fenced and patrolled against trespass. Two lakes, Bass and Norway, lie to the southwest in Clare County. Bass

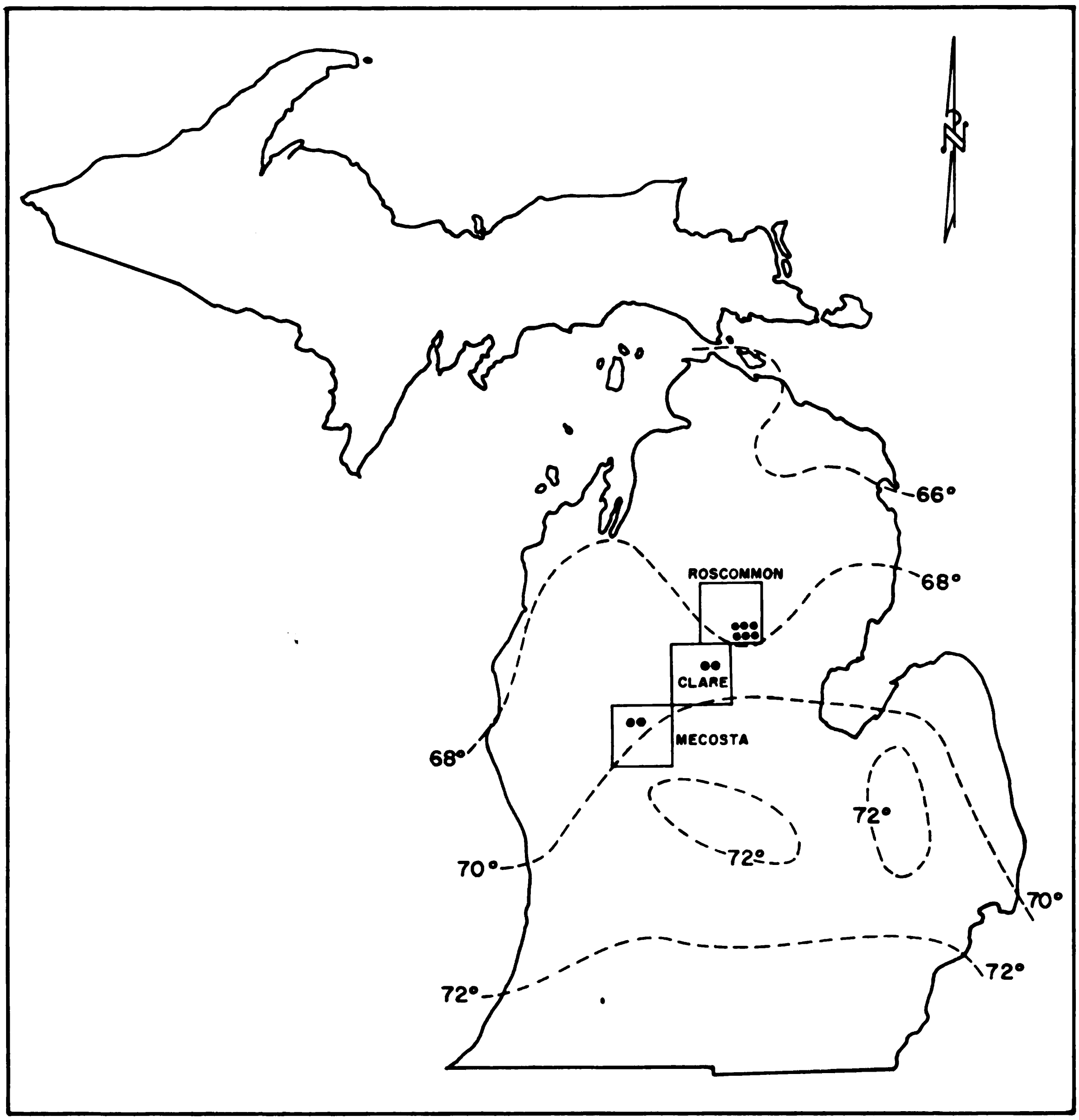


Fig. 2. Location of lakes in rainbow trout experiment relative to the 70 F isotherm (average July temperature).

Lake is on the Tobacco River Rod and Gun Club property; Norway Lake lies on the Cornwall Ranch. The remaining two lakes are in Mecosta County. These lakes, North Twin and South Twin, are located about 100 yards apart on the Larry Lewis Farm.

The investigational work on these private lakes was conducted under a contract agreement. This procedure was well accepted by the landowners. It provided me an experimental facility that was not available (limited fishing) on public lands. A copy of the contract agreement for 1960 is included in Appendix A.

The six Mid-Forest Lodge lakes lie in the extensive sand-plain area of northern lower Michigan (Veatch, 1953). The terrain surrounding the lakes is a glaciated upland of outwash and moraines ranging in elevation from 1, 200 to 1, 300 feet. The local topography varies from undulating to hilly. The main soil types are Roselawn and Rubicon (deep infertile sands of high permeability) on the uplands, with poorly drained sands, peat and muck in the limited lowland areas. There is no well defined surface drainage except that Ryan Lake constitutes the source of Denton Creek. Most of the area was originally covered with dense forests of white pine on the wet lowlands grading to red pine on the dry uplands, with scattered groups of hard-woods. At present the area is predominantly covered with aspen, oak and jack pine, with tag alder and white birch on the wet lowlands.

Bass and Norway, the Clare County lakes, lie in the morainic region on the southern edge of the Roselawn sand complex. The area surrounding the lakes is hilly with numerous swamps and potholes. The immediate terrain is infertile, gravelly sand, but about one mile to the south, heavier and more fertile soils predominate. Bass Lake has an intermittent drainage connection to other waters of the Tobacco River system through cedar and tag alder swamps. Norway Lake occupies a small pothole in a Roselawn sandy soil area with no surface drainage. The surrounding land is covered with an aspen-oak forest.

In the Mecosta County area, North Twin and South Twin are located in the Montcalm-Coloma association of soil types. The topography of this area is morainic and till plain. Local types are diverse with many quite fertile farms intermixed with hilly sand areas and numerous swamps. Pothole lakes and swamps are a feature of the landscape throughout the area. A small stream connects these lakes to two other small lakes within a distance of two miles. These drain to the Muskegon River system. Seepage waters here originate from land of much higher fertility than either the Clare County or Mid-Forest Lodge lakes.

Only a general description will be given here to introduce the character of the individual lakes. A detailed discussion and summary of the salient physical, chemical, and biological features of each lake is provided later. A map of the lake basins showing surface acreage and depth contours is provided in Figure 3.

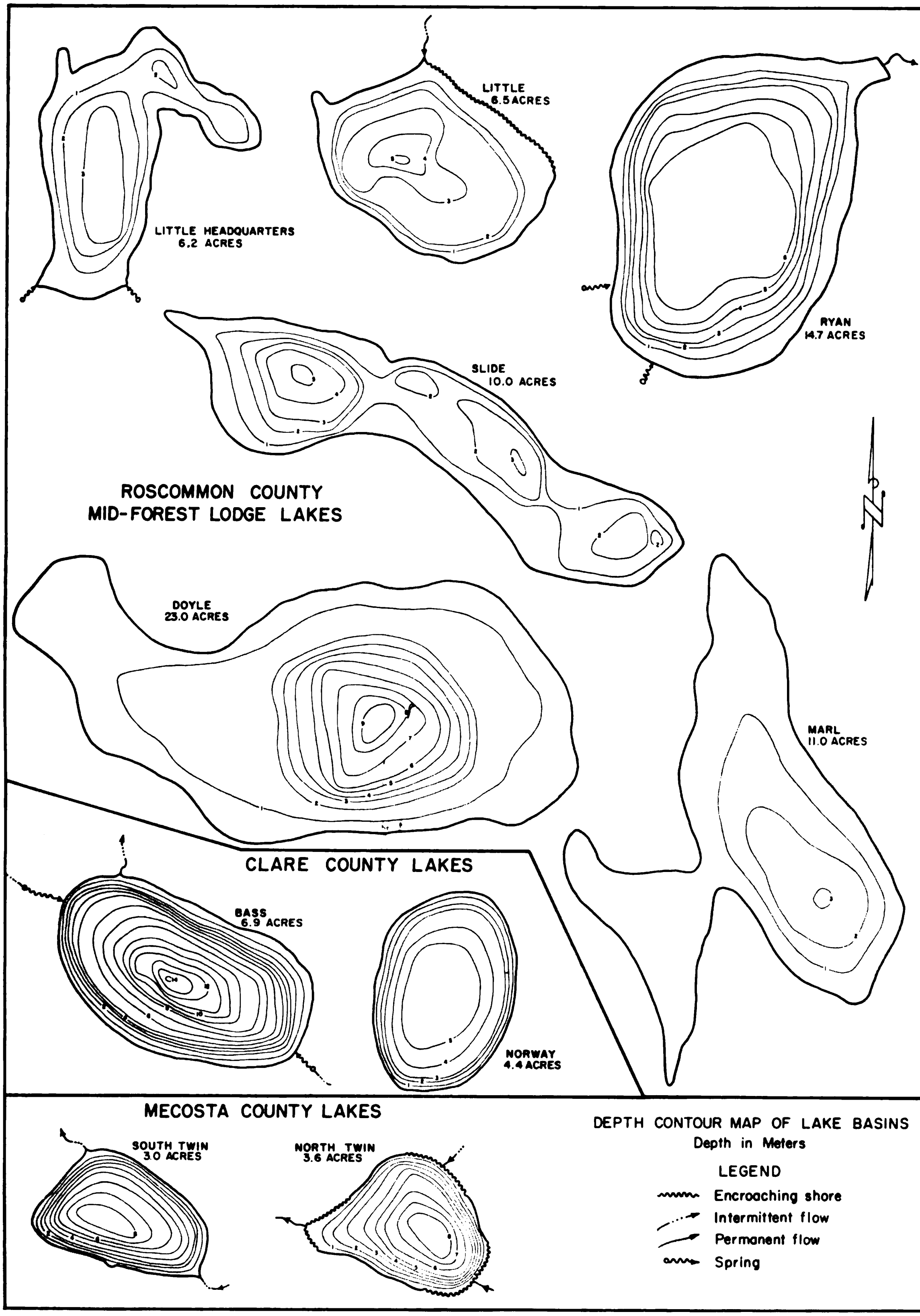


Fig. 3 Contour map of the ten lake basins.

Mid-Forest Lodge Lakes, Roscommon County

Three of the Mid-Forest Lodge Lakes, namely, Little Headquarters, Marl, and Slide are similar in several features. All are shallow, unstratified, clear or colorless, contain Chara as the dominant aquatic plant, and precipitate marl. A Secchi disc can be seen to the bottom even in the deepest water throughout the season. Little Headquarters Lake has a number of nearby cottages and is the scene of much human activity. Marl and Slide are remote forest lakes, generally visited only by fishermen.

The original fish population (prior to 1959 rotenone treatment for each lake) of Little Headquarters Lake consisted of golden shiners, bullheads, yellow perch and pumpkinseed sunfish. Slide Lake, surprisingly, contained no fish prior to the trout introduction. Marl Lake was populated only with small yellow perch.

The remaining three Mid-Forest Lodge Lakes, namely, Doyle, Ryan and Little have a light brown water color, are stratified and support fairly abundant growths of aquatic plants. The lake bottoms are soft, pulpy peat throughout the basins. Little Lake is quite soft with a methyl orange alkalinity of 20 ppm. Doyle and Ryan are moderately hard (70 ppm methyl orange alkalinity). Doyle Lake and Little Lake have extensive shoal areas; Ryan Lake has a sharp drop-off from shore to deep water and a relatively small shoal area.

The original fish population of Doyle Lake consisted of small bluegills and redbelly dace. Largemouth bass were introduced in the past but none were found in 1959. Ryan Lake contained many species of fish; the dominant species were bullheads, black crappies, yellow perch, pumpkinseed sunfish and northern pike. Little Lake contained only small pumpkinseed sunfish and redbelly dace.

A light winterkill occurred on Doyle, Marl and Little lakes in the severe 1958-59 Michigan winter.

Clare County lakes

Bass Lake is the deepest lake of the ten and could be considered a "two-story" or classical trout lake with some oxygen down through the thermocline. The water is colorless and markedly stratified. Originally the lake provided fairly good fishing for bluegills and largemouth bass. About ten species of fish were taken in the 1959 rotenone treatment.

Norway Lake is a rather unusual lake because the water is soft and of a perpetual deep green color. The high pH (9.0-10.5) and supersaturated dissolved oxygen content throughout the ice-free season result from a continuous algae bloom. Norway Lake, although shallow, is well protected from wind action and markedly stratified. The lake contained only a few bullheads, yellow perch and bluegills in 1959. According to the owner it has not produced fish of catchable size since the 1800's and has seldom been fished.

Bass Lake is the site of three permanent residences. Norway is a remote forest lake.

Mecosta County lakes

South Twin and North Twin lakes are hard-water lakes. Both are deep, highly stratified, and possess a narrow littoral zone. These lakes have extensive beds of Ceratophyllum out from shore to a depth of 5 to 10 feet.

South Twin is clean, but North Twin Lake is heavily polluted with blood from a shoreline slaughterhouse. In prior years North Twin also received the offal of the slaughterhouse and served only as a sewage lagoon. The lake is characterized by frequent heavy plankton blooms and periodic oxygen depletion. Populations of Cladocera and other zooplankton are high most of the time throughout the ice-free season. Apparently oxygen depletion is a frequent occurrence at the time of the fall overturn and in the winter, with consequent fish kills.

Both of these lakes contained numerous species of fish. South Twin Lake, in the opinion of the owner, furnished good fishing for bass and bluegills.

In summary, only Little Headquarters, Ryan, Doyle, Bass and South Twin lakes contained catchable game fish in 1959. Of these, only Bass and South Twin lakes were considered to provide fair to good fishing.

ESTABLISHMENT OF TROUT POPULATIONS

The field work of this study was conducted in the years 1959, 1960 and 1961. The general procedure followed was the stocking of hatchery rainbow trout in April and May following a chemical decimation of existing fish populations by rotenone poisoning. The stocked fish were subjected to the environmental conditions in each lake for one ice-free season. In late October the remaining numbers of fish were estimated when the lakes were again treated with rotenone. During the season, data were collected on trout growth, condition (K), survival, and causes of mortality to compare with data collected on chemical, physical, and biological factors of each lake. The methods used for the collection of these data are presented in the pertinent sections of this report.

The first year of field investigation (1959) was of value mainly in developing experimental techniques and in the gathering of survey information. Trout were stocked in all of the lakes in 1959. Apparently the lower waters of the highly stratified, deep lakes had not detoxified from the early spring rotenone treatment because a high initial mortality of the rainbow trout occurred. No dead trout were found but the low concentrations of rotenone believed to be present probably resulted in a slow, inconspicuous mortality. All ten lakes were repoisoned with rotenone in October of 1959.

The field work of 1960 provides the bulk of the data for comparison of success of the trout population in the ten lakes. The next sections of this report are based on the 1960 investigations. Reference is made to the 1959 work only to clarify the 1960 findings.

Field investigations in 1961 were restricted to studies of the effects of non-trout competition and differing population densities of trout on rates of growth.

The plants of trout

Both legal[2] and fingerling rainbow trout were planted in each of the ten experimental lakes in 1960. The legal trout were introduced in three distinguishable groups. One-half of the legal trout in each lake were stocked during the week of April 17 to 23. These fish were not marked by a fin clip and were designated as the no-clip (NC) group. The other one-half of the legal trout were planted during the week of May 22 to 28. These trout were made up of two groups, each comprising one-fourth of the numbers of the total legal plant. The first group was obtained from the Paris, Michigan, hatchery and marked by removal of the anal fin (designated A group). The second group was from the Wolverine Rearing Ponds and marked by removal of the left pectoral fin (designated LP group). The fingerling (young-of-the-year) trout were planted as a single group in each lake. They were planted during the week of May 22 to 28, in numbers approximately equal to the

---

[2]"Legal" trout in this sense refers to trout planted at an initial length of 7 inches or greater.

total plant of legal trout. Experience from the 1959 field work indicated that size differences alone were sufficient for identification of fish planted as fingerlings, so they were not marked by fin removal.

The trout in each of these four plants were carefully selected for uniform size by the hatchery personnel and placed in holding tanks prior to shipment. I then intensively sampled each group to determine the mean length, weight and condition factor (K). The estimate of variance of each measurement was very low and is omitted here. The results were as follows.

Table 1. Size of trout when planted, 1960

Group	NC	A	LP	Fingerlings
Length (cm)	20.9	21.6	20.4	4.8
Weight (g)	87.0	98.0	84.0	1.14
Condition factor	.953	.973	.989	--

These initial measurements formed the base for all growth calculations when the trout were recovered from the lakes in later collections. A summary of the number of trout planted in each group in each of the ten lakes is provided in Table 2.

The number of trout planted was intended to be at the rate of 100 legal and 100 fingerling fish per surface acre of each lake. It was

Table 2. Summary of numbers of rainbow trout stocked, 1960

Lake	Legal NC April 20[1]	Legal A May 24	Legal LP May 24	Finger-ling May 24
Little	275	137	137	549
Little Hdqrs.	290	125	125	500
Marl	389	175	175	700
Doyle	1, 190	575	575	2, 300
Slide	549	255	255	1, 020
North Twin	206	80	80	327
Bass	335	167	167	669
Norway	238	110	110	440
South Twin	195	75	75	305
Ryan	760	360	360	1, 440
Total	4, 427	2, 059	2, 059	8, 250

[1]From 0 to 40 NC fish were released in each lake from the mortality-check crates on May 15, 1960. These fish are included here.

later found that changes in water levels and errors in the scale of the aerial photographs used for mapping proved the original calculations of surface acreage to be inaccurate. Hence, the planting rates (recomputed) were somewhat variable.

Test of initial survival

After the 1959 experience of heavy initial mortality, I decided to determine any similar mortality in 1960 by direct observation. The procedure adopted was to place two live crates in each lake to provide for two independent samples. These crates were 2 x 2 x 4 feet in dimension, and built from 1/2"-mesh hardware cloth. In the stratified lakes they were anchored in the greatest depth of water containing 5 ppm of dissolved oxygen. In the shallow lakes they were suspended at a depth of about 10 feet.

At the time of the April plant, 20 trout from the NC group were placed in each of the two live crates. A daily record of mortality was taken for 21 days, following which the survivors were released. This procedure was duplicated in each of the ten lakes. A similar procedure was followed for the May plants except that 10 trout of the A group and 10 of the LP group were placed in each crate. These trout were not released after 21 days, but were left in the crates and used for other observations.

Table 3 is a summary of the data obtained from the live crates. It was evident that no initial mortality of consequence was experienced

Table 3. Numbers of 20 trout surviving 21 days in each of two live crates to check initial survival, 1960

Lake	April plant Live box A	April plant Live box B	Success of plant	May plant Live box A	May plant Live box B	Success of plant
Little	0	0	Failure[1]	17	16	Successful
Little Hdqrs.	20	20	Successful	20	20	Successful
Marl	20	20	Successful	19[2]	19	Successful
Doyle	20	20	Successful	20	20	Successful
Slide	20	19[2]	Successful	20	20	Successful
North Twin	20	19	Successful	0	1	Partly successful[3]
Bass	20	20	Successful	20	20	Successful
Norway	8	12	Successful[4]	17	13	Successful[4]
South Twin	20	20	Successful	20	19	Successful
Ryan	20	20	Successful	20	20	Successful

[1] April plant failed due to residual rotenone toxicity. May plant was not affected by rotenone.

[2] One trout died as result of handling injury.

[3] Polluted lake. Significant mortality of free-living trout.

[4] Trout in live crates died when pH rose above 10.5. Mortality did not extend to free-living trout.

in eight of the lakes after the April plant. The Little Lake fish experienced a complete mortality from rotenone toxicity again in 1960. The lake had remained toxic from the treatment in October, 1959. However, the lake did detoxify before the second plant was made in May. In Norway Lake, trout died in the live crates whenever the pH rose above 10 which happened on bright sunny days. Apparently few of the free-swimming fish died, as determined by later collecting.

Initial survival of the second (1960) plant of trout was high in nine of the ten lakes. In Norway Lake some of the trout in live crates died during periods of high pH (10.5), but it is doubtful if a significant number of the free-living trout died, as subsequent collections indicated no such loss. Some trout died in the live crates in Little Lake but not from rotenone toxicity as did the trout in the April plant. The mortality in May resulted from lack of oxygen (asphyxiation) when the crates were placed accidentally in deep water with low oxygen content. In North Twin Lake, however, a heavy loss of fish in the lake was in evidence both in the live crates and in the free population. This mortality was due to a severe oxygen depletion resulting from an effort to artificially circulate the lake with a stream of compressed air. Surface dissolved oxygen levels declined to a measured 1.4 ppm. Many of the trout were observed seeking refuge in the Ceratophyllum weed beds along shore where oxygen levels were as high as 7.0 ppm during the day.

The mortality in North Twin Lake from this oxygen depletion was estimated at 100 of the 359 legal trout planted. This was a very rough estimate; a precise count of dead fish was not possible due to the high turbidity of the lake and the rapid removal of carcasses by turtles.

In live crates in North Twin Lake, 39 of the 40 rainbow trout died immediately after the dissolved oxygen dropped to approximately 1 ppm. One trout survived oxygen levels of 0.6 to 1.6 ppm for 3 days and was still alive when levels of 5 ppm were restored about a week later.

Initial mortality can be summarized as consequential on two lakes. In Little Lake the entire 275 trout of the NC group were lost from residual rotenone toxicity. In North Twin an estimated 100 trout were lost from the NC, A, and LP groups combined, from an induced oxygen depletion. Some slight loss of trout may have occurred in the poorly buffered, highly alkaline waters of Norway Lake. The remaining lakes exhibited excellent initial survival of the planted trout.

FINDINGS AND ANALYSIS

Each rainbow trout population in the ten experimental lakes was subject to a different environment. Some environmental differences were inherent in the lakes, others were created by the manipulation of the density and composition of the fish population. The lake environments were not static but changed in various ways throughout the season. In net effect, however, the environment of each lake influenced the growth, mortality, and quality of the planted trout and determined the degree of success of each population.

In this section the findings of the 1960 field investigations are analyzed first, relative to the success of the trout populations; and secondly, relative to the determination and description of environmental conditions in each of the lakes.

Trout Populations

Fish sampling

Collections of fish were made at intervals of 5 to 6 weeks in each lake to obtain data on trout length, weight, and condition. The trout taken by anglers and reported in the creel census were not used for growth calculations, as it proved impossible to get accurate measurements from the fishermen.

In each of the five routine collections the objective was to obtain 10 fish from each of the groups of trout to allow statistical tests for differences in rates of growth.

Overnight gill-net sets were employed as the general collection method. The standard 6' x 125' experimental gill net comprised of 25 feet each of five mesh sizes, 3/4", 1", 1-1/4", 1-1/2", and 2", was used throughout these collections. The depth at which each trout was caught was recorded to provide data on depths frequented by the rainbow trout. The nets were set in locations in which experience indicated the best catches could be obtained per unit of effort. However, many sets were made from which few trout were taken. It is believed that the depths at which fish were taken are probably representative of the depths frequented by the rainbows for each lake.

A few trout were collected in Little Headquarters, Marl, and Slide lakes in July 1960 with a 2, 500-watt, D. C. boom shocker, incidental to night observations of the aquatic environment with submerged lights. This operation revealed the presence of, and furnished some growth data on, fingerling trout that were too small to be taken by the gill nets.

At the conclusion of the study in October, each lake was gill-netted intensively for several days to collect as many specimens as possible for examination. Each lake was then treated with rotenone to remove the remaining fish in preparation for new studies the following season. The number of trout killed was estimated by the Petersen mark-and-recapture method.

The mark-and-recapture method involves a number of assumptions: 1) mortality occurs at the same rate among marked and unmarked trout, 2) the marked and unmarked fish are equally vulnerable to collection, 3) the mark is not lost, 4) the mark is recognized and reported, and 5) the marked fish are randomly mixed in the population (Ricker, 1958).

To meet these conditions as nearly as possible, the following procedure was used. A known number of 7- to 12-inch hatchery trout were marked by removal of the dorsal fin and were released in each lake. These trout were scatter-planted about the lake 24 to 48 hours prior to rotenone treatment. From 50 to 100 marked trout were used in each lake depending upon lake size. As large a sample as possible of trout surfacing in distress was collected. To these were added all trout found dead for a two-day period after the poisoning. Population estimation was then computed from the proportion of dorsal-clipped fish in the entire collection.

I believe that this procedure meets all of the assumptions of the method with one exception. The dorsal-clipped fish may have been more vulnerable to collection than the unmarked (NC, A, and LP groups) as it was my observation that they were more easily picked up when surfacing in distress from the rotenone. If the dorsal-clipped fish were more vulnerable to collection, the method would tend toward a low estimate of the population. I believe the magnitude of this possible error is negligible because the subsequent collection of dead fish after the poisoning would tend to correct any bias that might have occurred.

A total of 2, 514 of the 8, 240 legal trout planted were captured for use in the growth studies. A summary of these collections is presented in Table 4.

Fingerling trout

Fingerling trout were stocked in numbers equal to the legal trout in each lake. The one outstanding characteristic of the fingerling plant in all lakes except Little Headquarters was the extremely high rate of mortality. In the nine lakes the fingerling mortality amounted to about 99 percent. It is not known when the mortality occurred but it is probable that initial mortality was high as very few fingerling trout were observed in any lake except Little Headquarters.

Table 4. Numbers of trout from each group collected and used in growth calculation, 1960

	Little Hdqrs.	Ryan	Doyle	Little	Marl	Slide	Bass	Norway	South Twin	North Twin
NC group										
May	26	14	8	--[1]	16	9	9	10	--	3
June	19	23	28	--	16	25	33	37	13	9
July	22	17	12	--	25	24	26	25	24	5
September	11	9	17	--	6	9	16	21	14	4
October	34	85	121	--	54	159	71	44	80	9
Sub-total	112	148	186	--	117	226	155	137	131	30
A group										
June	15	12	18	18	12	14	2	8	5	5
July	5	17	8	17	11	10	16	6	10	5
September	10	5	6	5	2	2	10	5	3	1
October	18	59	85	22	21	71	41	19	38	8
Sub-total	48	93	117	62	46	97	69	38	56	19
LP group										
June	9	9	17	14	8	8	7	5	8	2
July	9	12	13	15	14	5	13	5	13	8
September	5	0	5	10	1	2	3	5	6	1
October	28	52	74	27	11	89	42	23	34	14
Sub-total	51	73	109	66	34	104	65	38	61	25
Total	211	314	412	128	197	427	289	213	248	74

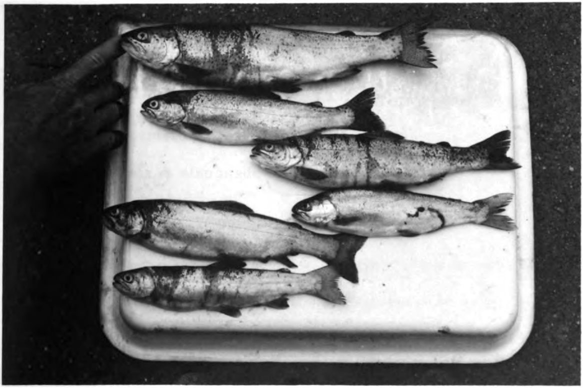
[1] 100% mortality from rotenone toxicity when planted.

Fig. 4. Rotenone treatment of Bass Lake.

Fig. 5. Method of collecting fish in distress at time of rotenone treatment.

Fig. 6. Gill-net collection of trout from Bass Lake, July 30, 1960. Fish are arranged on table according to NC, LP, and A groups. Note uniformity of size of each group.

Fig. 7. Comparison of trout from Bass Lake and Norway Lake, July 1960. Larger fish of each pair is from Bass Lake. Upper pair, NC group; center pair, A group; lower pair, LP group. Note the conspicuous difference in size between lakes. Also note lack of regeneration of the clipped anal and left pectoral fins in this figure and Figure 6 above.



The fingerling trout planted were very small. The mean length when planted was 4.8 centimeters and the average weight 1.14 grams.

In Little Headquarters Lake the seasonal mortality rate was .736. Forty-two of the 500 planted were recovered in the growth collections. One hundred and ten fingerlings were recovered in the final rotenone poisoning, and an additional 22 were estimated present. There is every indication that these fish would have made a significant contribution to the 1961 catch if they had been allowed to remain in the lake.

Fortunately, enough fingerlings were captured in Little Headquarters Lake to determine periodicity of growth. Growth in length is shown in Figure 8. Actually the rate of growth was fairly rapid; the mean length equalled the Michigan legal size (7 inches) in early October.

A few fingerlings were recovered in Slide (10 individuals), Little (22), Doyle (3), Bass (12) and North Twin (1) in the final rotenone treatment. All of these fish were noticeably smaller than those taken in Little Headquarters Lake. A comparison of the final size based on these limited data is also made in Figure 8.

Differential growth of trout

The first population parameter of trout success that I will discuss is growth as expressed by the total increase in weight of individual trout for the season. The trout in the final collections varied little in size between the NC, A, and LP groups, but considerably

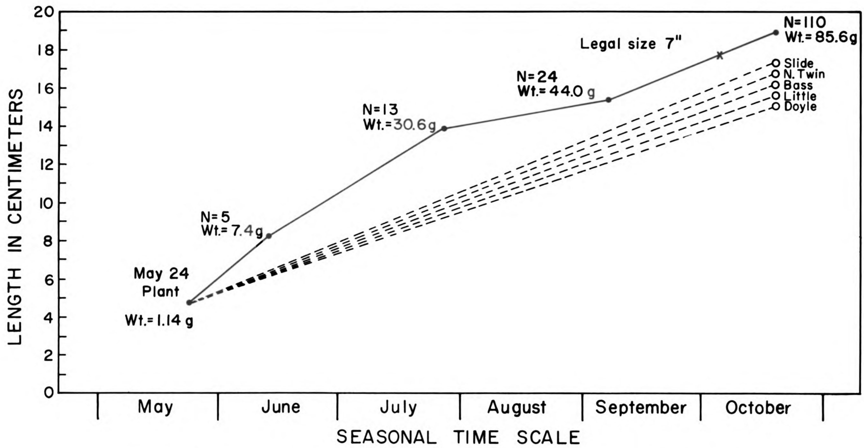


Fig. 8. Growth of rainbow trout fingerlings, 1960. Solid line represents growth in Little Headquarters Lake, broken lines indicate comparison of fingerling trout growth in other lakes.

Fig. 9. Comparison of trout size between Little Headquarters and Ryan lakes, 1960. The trout on left are legals from Little Headquarters, in the center corresponding legals from Ryan, and on the right fingerlings from Little Headquarters. The fingerlings were stocked at 4.8 cm in length and are a year younger than the other two groups.

Table 5. Mean weight (grams) and length (centimeters) of each group of trout at end of season, October 1960

Lake	No clips		Anals		L. pectorals		Fingerlings	
	Weight	Length	Weight	Length	Weight	Length	Weight	Length
Little	--	--	282.4	29.2	256.3	28.2	52.8	15.9
Little Hdqrs.	290.6	30.1	257.8	29.0	262.9	29.1	85.6	19.0
Marl	290.6	30.2	246.7	28.7	232.3	28.0	--	--
Doyle	279.0	30.3	246.2	29.2	246.9	29.1	44.0	15.1
Slide	260.4	29.2	231.8	28.1	228.7	28.0	70.6	17.4
North Twin	286.2	30.3	225.5	28.3	196.7	27.6	50.0	16.8
Bass	227.2	29.0	197.3	27.7	178.7	27.0	49.3	16.3
Norway	174.0	26.2	161.8	25.2	150.4	25.2	--	--
South Twin	149.0	25.4	154.8	25.8	135.8	24.6	--	--
Ryan	112.1	23.7	119.1	24.0	100.5	23.0	--	--

between lakes. The final mean length and weight of each group from each lake is summarized in Table 5. The difference in final size of the trout was of considerable magnitude; the trout in Little Lake weighed about 2.5 times more than those in Ryan Lake.

To test the significance of the differences in size of the trout between groups and between lakes a two-way analysis of variance was computed using the total increase in weight increment of the individual trout. In making this test the NC group was deleted, so the difference between groups was restricted to the A and LP groups. The NC group was deleted because they suffered a complete mortality in Little Lake, and also because this group of trout were planted five weeks earlier than the A and LP groups, so the growth in weight increments were not directly comparable.

Table 6. Results of the two-way analysis of variance test of growth in weight increments between groups and between lakes

Source	Sum of squares	Degrees of freedom	Mean square	F^1	$F_{.95}$	$F_{.99}$
Lakes	52,219.45	9	5,802.16	93.1^{++}	3.18	5.35
Groups	.13	1	.13	$.002^{-}$	4.96	10.04
Error	560.83	9	62.30			
Total	52,780.41	19				

[1]Statistical significance at the .99 confidence level is indicated with two plus signs (++), the .95 confidence level with one plus sign (+), and any probability or confidence level below .95 with a small dash (-).

The difference of growth in weight between the A and LP groups was thus negligible in these ten lakes. Although minor differences in growth occurred by chance between the groups in individual lakes, the difference between groups was almost nil between the ten lakes. The actual mean weight growth increment for the A group was 114.46 grams, and for the LP group 114.62 grams for the ten lakes. The seasonal growth curves of the A and LP groups are compared with the seasonal growth curve of the NC group in Figure 10. The three groups of trout grew at almost parallel rates throughout the 1960 season.

The difference of growth in weight of the trout between lakes was highly significant at the one percent level of confidence. It is apparent, therefore, that the differences in the final size of the trout in the various lakes was due to influences of the environment on rates of growth, rather than to chance variation within the trout groups in each lake.

With the information at hand that significant differences exist in the final weight of the trout among the ten lakes, it is desirable to determine the significant differences between the individual lakes. The best estimate is to make all possible comparisons between the means of the individual lakes. This was accomplished by combining the A and LP groups and computing a one-way analysis of variance (multiple range test) between the lakes. The following significantly different sub-groups arranged in the order of descending weights were found using Duncan's (1955) Significant Studentized Range Tables at the one percent level:

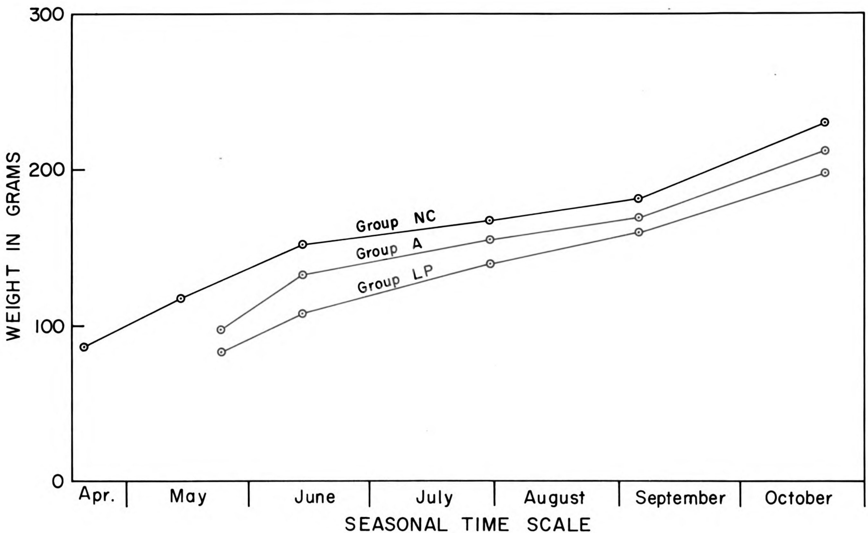


Fig. 10. Seasonal gain in weight of the three distinct sub-groups of rainbow trout, 1960.

Little
Little Headquarters
Doyle
Marl
Slide
North Twin
Bass
Norway
South Twin
Ryan

At the less discriminating five percent level of confidence the following significantly different sub-groups were found using either Duncan's or Snedecor's (1956) Q tables:

Little
Little Headquarters
Doyle
Marl
Slide
North Twin
Bass
Norway
South Twin
Ryan

In following discussions of trout success the lakes will be listed in the above order on the basis of growth in weight. The significantly different sub-groups indicate that no lake can shift over one rank up or down at the five percent level of confidence, and only Little Headquarters and Marl lakes can shift two ranks at the one percent level. No single comparisons of growth rates will be made within the same sub-groups as listed above.

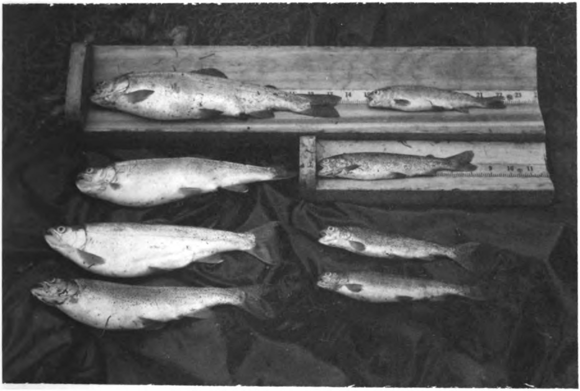
Condition factor

The condition factor (K) of the trout can be used as a measure of trout success. Condition factor in this instance is computed $K = \frac{100\ W}{L^3}$ (weight in grams, length in centimeters); K is simply a measure of robustness of the fish. The condition factor is closely related to the rate of growth of the fish as has been found by Brown (1946), Hansen (1951), and Cooper (1953). The greatest value of K in determining trout success in this study is the additional validation it lends to growth rates throughout the season. High values of K (1.00+), as a direct measure of robustness, can be considered as an indication of the general well-being of the trout.

The NC groups of fish planted in April showed both an increase in weight and a corresponding increase in condition factor by mid-May. This indicates that they took food immediately after planting and adjusted quickly to the lake environment (Table 7).

Throughout the growing season the rate at which trout grew in absolute weight was closely related to condition factor. In Little Lake,

Fig. 11. Growth of legal trout in Little Headquarters Lake, 1960. The larger fish were collected from the lake at the end of the season in October. The smaller fish are fresh hatchery specimens selected to equal the size at which the larger fish were planted in April and May.



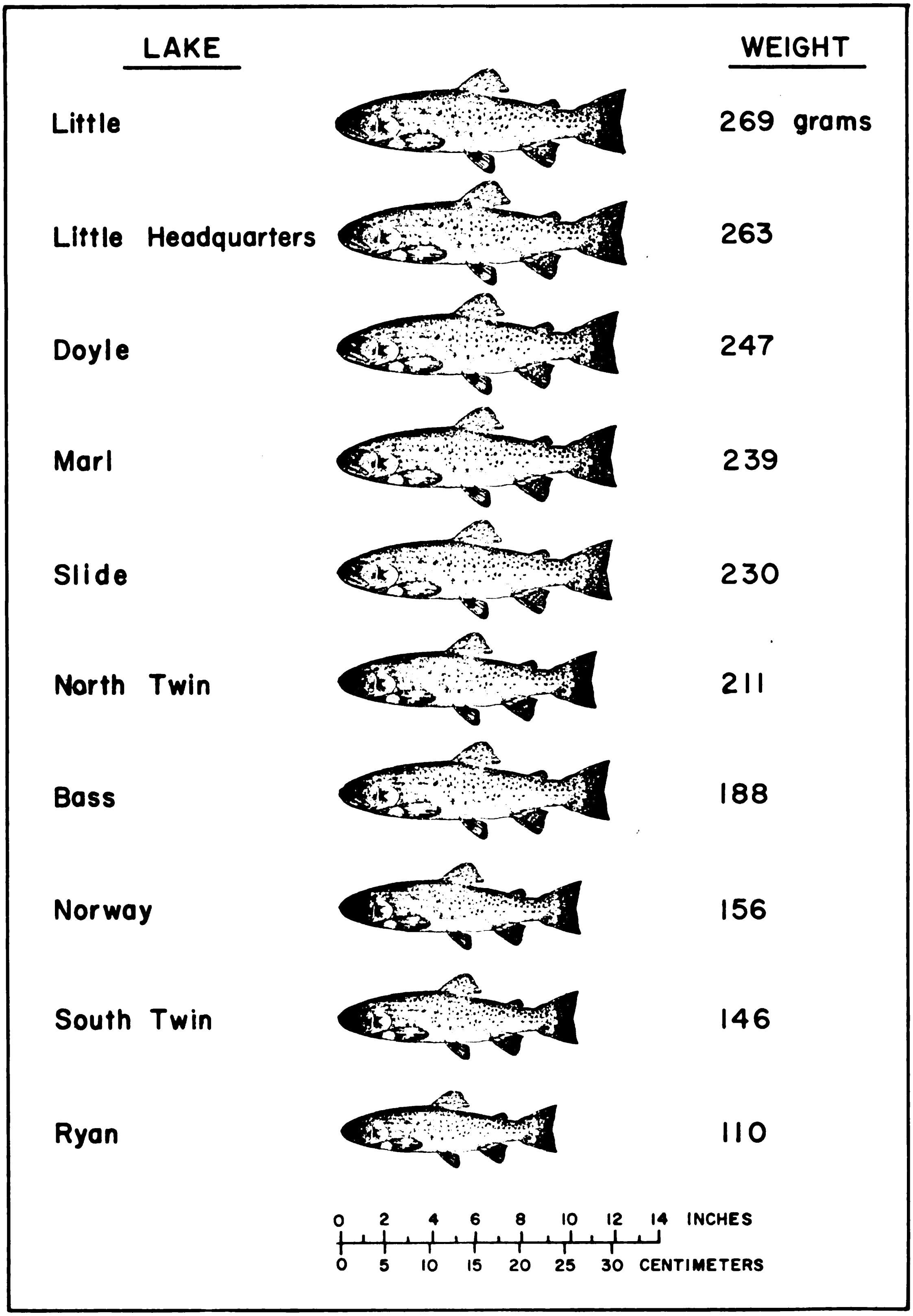


Fig. 12. Graphic comparison of the final size of the rainbow trout in each of the ten lakes, 1960, based on the mean weight of the combined A and LP groups.

Table 7. Summary of condition factor (K) for rainbow trout, 1960

Lake	NC group	NC group	All groups					Average
	April[1] 20	May 14	May[2] 24	June 14	July 30	Sept. 5	Oct. 20	June to October
Little	--	--	.981	1.013	1.035	1.100	1.093	1.061
Little Hdqrs.	.953	1.016	.993	.957	1.047	1.029	1.066	1.025
Marl	.953	1.015	.992	.962	.976	.980	1.052	.992
Doyle	.953	.975	.979	.959	.993	1.050	.999	1.000
Slide	.953	1.030	.997	1.021	1.007	1.015	1.043	1.022
North Twin	.953	.929	.964	1.040	1.046	.950	1.004	1.010
Bass	.953	1.000	.987	1.005	1.023	.959	.928	.979
Norway	.953	.932	.965	.960	.953	.918	.975	.952
South Twin	.953	--	.981	1.031	.900	.898	.907	.934
Ryan	.953	.896	.953	.956	.875	.852	.844	.884

[1] K of NC group at time of plant.

[2] K influenced by May plant of A and LP groups in all lakes.

for example, both the increase in weight and condition factor were high throughout the season. In Bass Lake the trout grew most rapidly in June and July. The condition factor increased from .987 in May to a high of 1.023 in July. From July until October the condition factor declined to a final value of .928. This decline in K, without a compensating growth in length, was sufficient to cause production[3] in September and October to be a negative value. A similar negative production during some period of the season was also noted in Ryan, North Twin, and Marl lakes according to the empirical growth data.

The regression between condition factor and total increase in weight for the entire population was computed. The correlation coefficient (r) of this regression was $r = .876^{++}$.

Periodicity of growth

This study was designed to obtain accurate information on the periodicity of growth in weight throughout the season. Each plant consisted of uniform-size trout in all lakes. These trout were selected for size at the hatchery to reduce variation to a minimum. Four gill-net collections were made at 5- to 6-week intervals throughout the season on each lake. Large samples of trout were analyzed when the trout populations were removed from the lakes with gill nets and rotenone at the end of the season. As discussed under differential growth, the three distinct sub-groups of trout (NC, A, LP) grew at

---

[3] Production is defined as the total elaboration of new body substance in a unit of time, irrespective of whether the organism survives to the end of that time (sense of Ivlev, 1945). Also called total production (Ricker, 1958), Net Production (Clark, et al., 1946).

parallel rates in each lake. The variation between sub-groups in mean size was less than the variation between lakes. Hence, the empirical mean weight of each trout collection is considered quite accurate even when allowing for all possible errors.

The mean individual weight of trout for each population is shown by synthetic seasonal curves in Figure 13. Trout of the second plant (in May) were smaller than those present in each lake from the April plant. The average weight of the individual trout in the May sample was thus reduced, causing a break in the growth curve.

The seasonal growth of the trout varied markedly between the populations in the ten lakes regardless of the final weight attained. In Little, Marl, Little Headquarters, Slide, North Twin and Norway lakes, the periods of rapid increase were in the spring and fall. In Bass Lake the trout grew most rapidly in June and July and actually declined in weight in the fall. In Doyle Lake the trout followed neither of these patterns, as they increased in size evenly throughout the season. In Ryan and South Twin lakes the growth was very slow throughout the season. These marked differences in the seasonal growth pattern are certainly due to differences in environmental conditions among the lakes. The specific environmental factors responsible for seasonal variation in trout growth will be discussed later.

The mean periodic weight increment along with the corresponding rate of instantaneous growth for 5-week periods throughout the season are provided in Table 8. These periodic growth values are

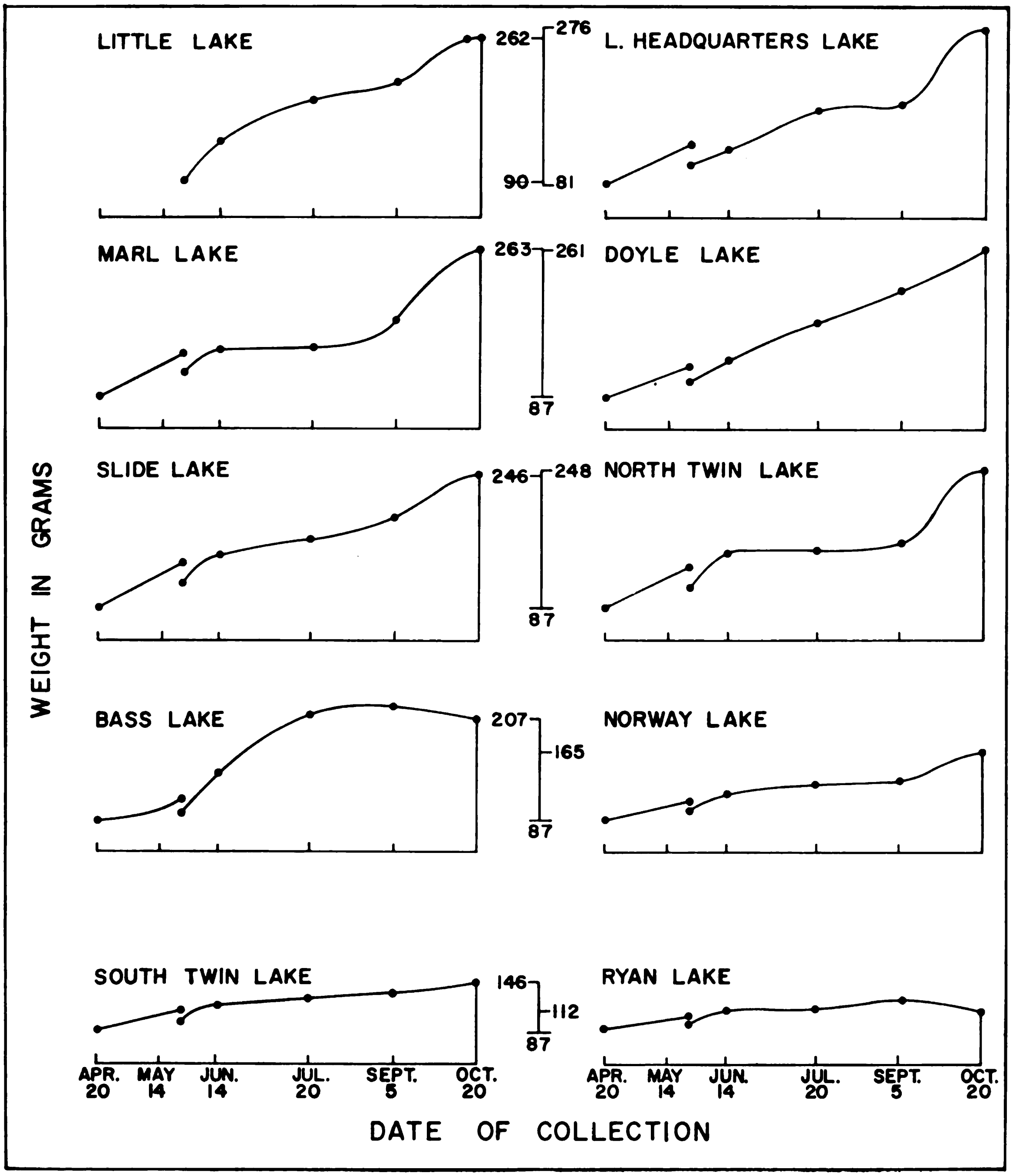


Fig. 13. Synthetic growth curves representing weight of individual trout in each (all groups NC, A, LP combined) of the ten populations, 1960.

Table 8. Growth increments in weight (grams) and instantaneous growth rates (*g*) for consecutive five-week periods in 1960

Lake	Periods										Total of incre-ments
	April 20 - May 21		May 22 - June 25		June 26 - July 30		July 31 - Sept. 3		Sept. 4 - Oct. 8		
	Weight	*g*	Weight	*g*	Weight	*g*	Weight	*g*	Weight	*g*	
Little	--	--	62	.52	34	.20	17	.09	56	.24	169
Little Hdqrs.	47	.43	35	.29	37	.23	7	.04	88	.39	214
Doyle	34	.33	35	.30	33	.22	31	.17	41	.19	174
Marl	51	.46	35	.27	-5	-.03	31	.20	86	.40	198
Slide	51	.46	41	.31	14	.09	22	.12	53	.25	181
North Twin	55	.49	48	.35	-3	-.02	2	.01	82	.41	184
Bass	29	.29	62	.49	55	.30	4	.02	-11	-.05	139
Norway	27	.27	24	.22	9	.07	0	.00	30	.21	90
South Twin	23	.24	26	.23	2	.02	4	.03	12	.09	67
Ryan	19	.20	20	.19	1	.01	7	.06	-5	-.04	42
Average weight increase	37.3		38.8		17.7		12.5		43.2		149.5

essential in establishing the dynamics of each population and in the computation of production to further evaluate trout success. Data on periodic growth of trout, however, is of value in its own right and will be discussed here.

Most fishery biologists accept the assumption of maximum growth of salmonids in the late spring and early summer (Hatch and Webster, 1961). Cooper (1953) found that brook trout in three Michigan streams grew most rapidly in May and June, and growth decreased during the remainder of the warm season. A histogram of the periodic growth data in this study is presented in Figure 14. Even with the large variance among lakes it is clear that the general pattern of rapid growth in these lakes is bimodal, i.e., spring and fall. The greatest increase in absolute weight accrued in September. An inspection of the instantaneous growth rate (Fig. 15) indicates the most rapid exponential growth relative to fish size at the beginning of the season in April and May, a decrease until August, and a sharp increase again in September. Bimodal spring and fall rainbow trout growth has also been reported by Johnson and Hasler (1954) for dystrophic lakes in Wisconsin. These authors concluded that high temperature adversely affected growth during July and August.

It has been concluded by some investigators that seasonal growth of certain fishes is controlled, at least in part, by endocrine secretions. One recent study (Gross, et al., 1963) found that growth in green sunfish was influenced by thyroid activity which in turn was

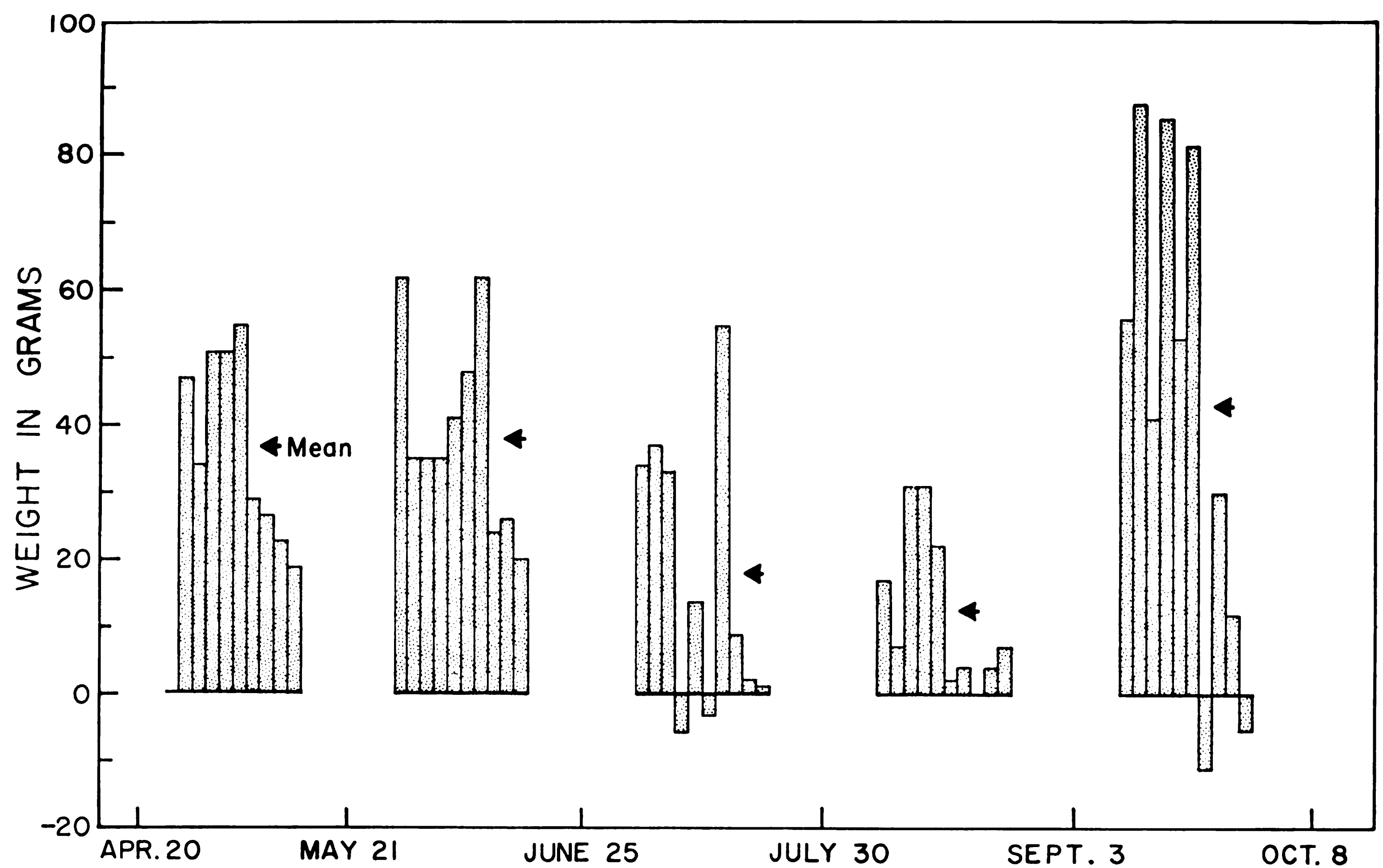


Fig. 14. Absolute growth increments for consecutive five-week periods, 1960. (Lake arrangement for each bar in histogram from left to right: Little, Little Headquarters, Marl, Doyle, Slide, North Twin, Bass, Norway, South Twin, Ryan)

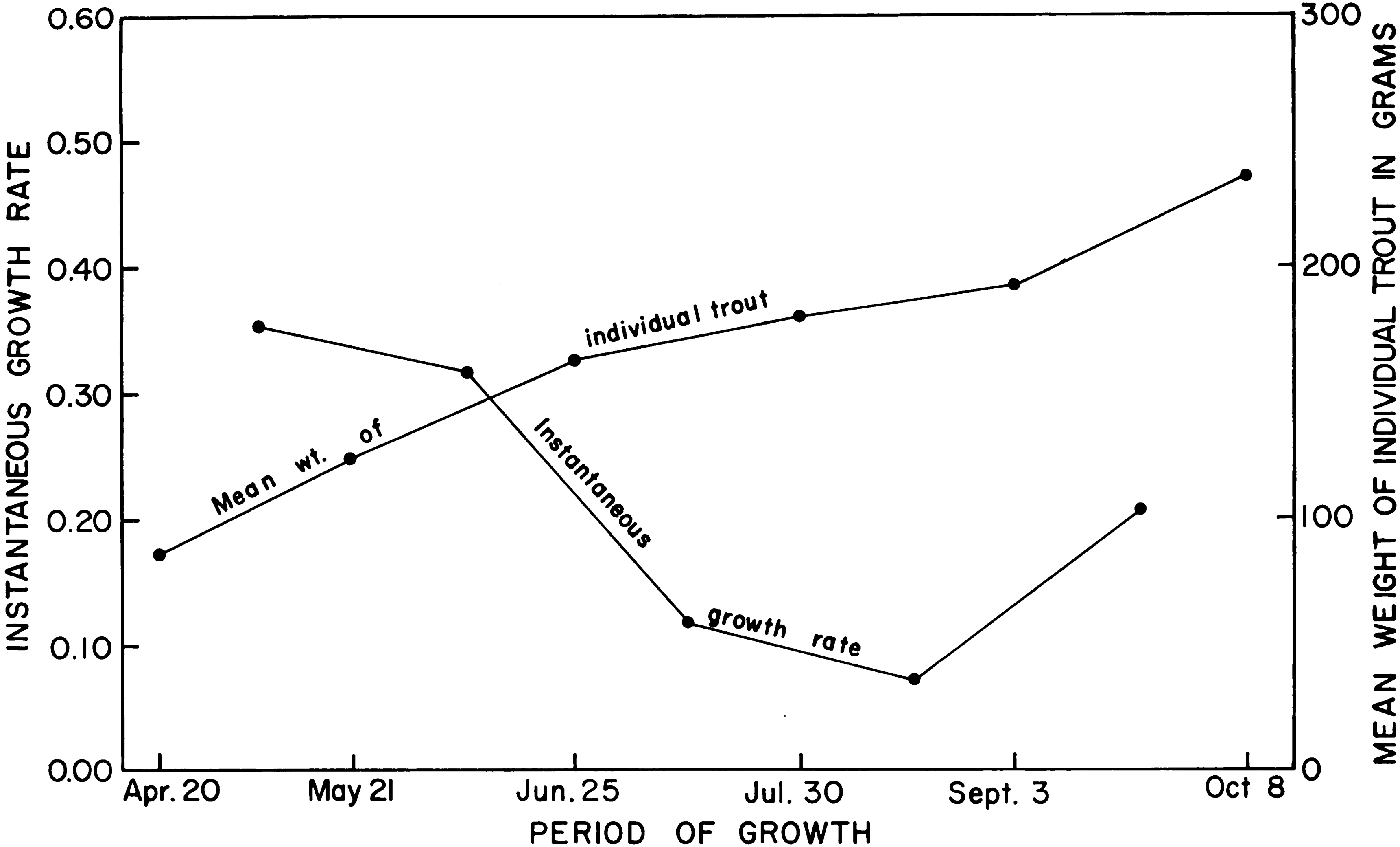


Fig. 15. Relationship of periodic absolute growth of rainbow trout to the instantaneous rate of growth for corresponding periods, 1960.

affected by the length of the daily photo period. Anderson (1959) fed bluegills in cages in a southern Michigan lake and in four constant-temperature laboratory cages at 50, 60, 70, 80 F for a 16-month period. He found that, although the fish in the laboratory aquaria grew faster in the winter months than did those in the lake cages, both groups grew most rapidly in May and June. Anderson concluded from this observation that a seasonal factor, most likely a growth hormone, appeared to operate with temperature to control growth.

The observations of this study lead me to conclude that rainbow trout growth would proceed at a constant absolute rate throughout the season with a corresponding logarithmic decrease in the instantaneous rate, except for the influence of temperature. There is no evidence of an endocrine mechanism operating to further influence growth.

In referring again to the synthetic growth curves in Figure 13, it is apparent that the trout in Doyle Lake grew at a nearly constant absolute rate throughout the season. This was not a chance occurrence as a relatively straight-line absolute growth rate was also observed in Doyle Lake in 1959 and 1961 (Fig. 24). In Bass Lake the trout grew most rapidly in June and July, with slow growth in August and September. South Twin, Ryan, and Little lakes also showed little or no tendency to bimodal spring and fall growth. All of these lakes are thermally stratified with cool temperatures (65 F) readily available to the trout at a depth of not over 4 meters at the time of maximum summer thermal stratification (Appendix Figs. 26 to 35). The trout in these lakes could escape high summer water temperature by descending to lower depths. Trout were taken at greater depths in July and August than in the spring or fall in the gill-net collections (Table 20), but it was found that they still ranged to the lake surface to seek food.

It was in the shallow lakes with no cool refuge area available that the bimodal growth pattern was most prominent. In Marl Lake the trout were exposed to warm temperatures by the extreme shallow depth (average depth 1 meter). In North Twin Lake the trout were forced into the 70 F surface waters by severe oxygen depletion at a depth of 2 meters during July and August. These two lakes showed the most well defined biomodal growth pattern. Little Headquarters and Slide lakes are also very shallow and exhibited the bimodal growth to only a slightly lesser degree.

In Figure 16 I plotted the periodic growth increments for Slide Lake against the seasonal temperature with synthetic curves. Slide Lake was selected for this example as it most nearly approached the mean periodic growth curve of the ten lakes. It will be noted that the growth rate in Slide Lake declined very rapidly as temperature rose from 65 to 70 F in June. Apparently the trout were able to acclimate somewhat to the warm water because growth began to increase in July when water temperatures were in the mid-seventies. The rapid increase in growth in September coincided with a drop in water temperature from 70 to 50 F.

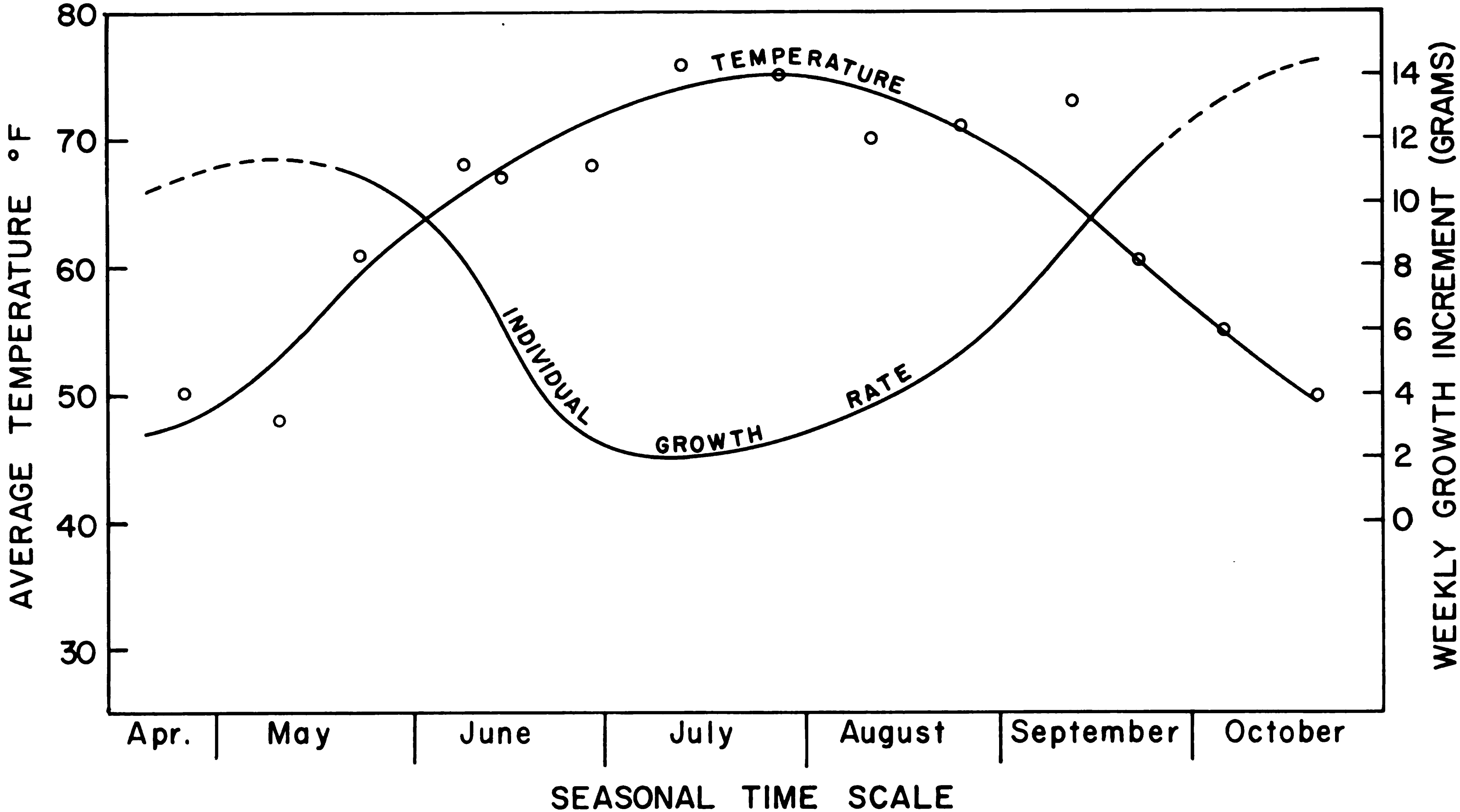


Fig. 16. Relationship between temperature and rate of growth of rainbow trout in Slide Lake, 1960.

Survival and mortality

Survival or its complement, mortality, is the population parameter that, along with growth, determines the success of a trout population. A high rate of mortality can be expected in any fish population. Cooper (1953) stated that the mortality rate of trout in natural populations is about 97 percent the first year, and 75 percent in succeeding years. In lakes where artificial populations of trout are established, such as in this study, no natural reproduction or recruitment of stock can be expected because the trout do not have suitable habitat to spawn. Populations thus experience a continuous depletion, the rate of which influences production by offsetting gains in weight and determines the total stock available to the angler.

Of the 8, 545 legal trout planted in the ten experimental lakes, the cause of mortality was determined for 5, 439 or 63. 6 percent of the total (Table 9). The remaining 3, 106 or 36. 4 percent of the trout disappeared without trace and are termed "unknown" or natural mortality. These figures are not exact but are close approximations.

Fishermen reported taking 1, 457 trout or 17. 1 percent of the total populations in the ten lakes. This figure may be slightly low although all anglers agreed to secure a fishing permit from the caretaker or lake owner and file it with a record of fish taken immediately after completion of the trip. I have no evidence to indicate that this was not done.

Table 9. Amount and source of legal trout mortality, 1960

Lake	Number trout planted	Source of mortality: Growth collections	Scavenger loss in gill nets	Lethal water	Angling	Rotenone (unrecovered)[1]	Total identifiable mortality: Number	Percent	Unidentifiable mortality: Number	Percent
Little	549	128	10	275	5	84	502	91	47	9
Little Hdqrs.	540	211	10	0	223	13	457	85	83	15
Doyle	2, 340	412	45	0	468	63	988	42	1, 352	58
Marl	739	197	100	0	60	51	408	55	331	45
Slide	1, 059	427	48	0	248	71	794	75	265	25
North Twin	366	74	14	111	0	40	239	65	127	35
Bass	669	289	50	0	201	60	600	90	69	10
Norway	458	213	20	0	0	97	330	72	128	28
South Twin	345	248	13	0	0	41	302	88	43	12
Ryan	1, 480	314	17	0	252	236	819	55	661	45
Total number	8, 545	2, 513	327	386	1, 457	756	5, 439	--	3, 106	--
Percentage of total	100.0	29.4	3.8	4.5	17.1	8.8	63.6		36.4	

[1] Estimated on basis of mark and recapture.

In the gill-net (growth study) collections, 2,513 trout or 29.4 percent of the total were processed. An additional 327 trout (3.8%) were estimated lost in the gill nets due to mutilation by turtles and crayfish; often only little scraps of fish tissue, or the head of the trout was left in the net. More often the head or tail section was eaten away so that no growth measurement could be made.

The NC group lost from rotenone toxicity in Little Lake contributed 275 trout to the known mortality. At North Twin Lake there was a mortality of trout due to oxygen depletion when I attempted artificial circulation of the lake with compressed air. Eleven dead trout were found at the outlet screen, and an additional 100 (±50%) was the estimated loss throughout the lake.

The method of population estimation in the final rotenone kill in October has been discussed previously under trout collection methods. The estimate of the unrecovered number of trout in all lakes was 756 or 8.8 percent of the total initial population. This unrecovered segment of the population was low because many trout were removed by intensive gill netting on each lake during the week just prior to the rotenone treatment. All trout taken in the October gill netting and those recovered in the rotenone treatment were included in the 29.4 percent of the population removed for growth collections. Together these sources account for the 63.6 percent total known mortality. The greatest chance for error in these estimates lies in trout taken but not reported in the creel census, and errors in the population estimates of

the final rotenone treatment. These errors are believed to be low in magnitude.

The 3, 106 trout not accounted for (36.4%) in the known mortality are designated natural mortality after the method of Ricker (1958). These trout account for 12 percent of the total population in South Twin Lake, the lowest natural mortality; up to 58 percent in Doyle Lake where the greatest natural mortality occurred. The probable causes of this natural mortality will be discussed later.

Natural mortality can be considered singly as a measure of trout success. The rate varies between lakes, which reflects the influence of responsible environmental factors. In Table 11 the total mortality of trout in each lake is divided on the basis of Ricker's equation $a = u + v$; where a = the annual rate of mortality, u is the fraction removed by fishing, and v the fraction lost by natural mortality. In Table 11 the fishing mortality (u) includes all trout mortality resulting from gill-net fishing as well as the catch by anglers. North Twin Lake is included but the true proportion of natural mortality is not accurately known.[4]

In Table 11 natural mortality as a fraction of the total trout population is provided in column v. Natural mortality as a portion of the entire population, however, is not valid for a comparison between lakes because it is influenced by fishing mortality, which is not constant

---

[4]For practical purposes North Twin Lake is so badly polluted that annual losses from summerkill and winterkill would reduce it to the lowest rank for the year.

Table 10. Total mortality (numbers of trout) and corresponding instantaneous mortality rate (*i*) for consecutive five-week periods in 1960

Lake	Number trout planted	April 20-May 21 Number	April 20-May 21 *i*	May 22-June 25 Number	May 22-June 25 *i*	June 26-July 30 Number	June 26-July 30 *i*	July 31-Sept. 3 Number	July 31-Sept. 3 *i*	Sept. 4-Oct. 8 Number	Sept. 4-Oct. 8 *i*	Total mortality	Seasonal mortality rate (a)	Number surviving Oct. 8
Little	275	--	--	52	.21	18	.09	46	.25	23	.16	139	.505	136
Little Hdqrs.	540	91	.38	142	.38	83	.32	94	.55	34	.30	444	.822	96
Doyle	2,340	388	.40	577	.35	613	.59	231	.36	162	.36	1,971	.842	369
Marl	739	115	.35	212	.42	90	.25	120	.47	54	.31	591	.800	148
Slide	1,059	59	.11	292	.35	110	.17	130	.25	68	.16	659	.622	400
North Twin	366	32	.17	146	.57	20	.11	40	.27	23	.20	261	.713	105
Bass	669	23	.07	103	.17	98	.20	50	.12	106	.31	380	.568	290
Norway	458	32	.14	89	.23	30	.09	67	.25	50	.23	268	.585	190
South Twin	345	6	.03	39	.12	62	.23	10	.04	31	.15	148	.429	197
Ryan	1,480	154	.23	308	.26	259	.29	184	.28	122	.24	1,027	.694	453

Table 11. Mortality and survival of rainbow trout, 1960. Decimal fractions of entire populations.

Lake	Total mortality (a)	Fishing mortality (u)	Natural mortality (v)	Surviving al (s)	Natural mortality of fish surviving after fishing $\frac{v}{v+s}$
South Twin	.43	.31	.12	.57	.17
Bass	.57	.47	.10	.43	.19
Little	.50	.33	.17	.50	.25
Slide	.62	.39	.23	.38	.38
Norway	.59	.32	.27	.41	.40
Little Hdqrs.	.82	.67	.15	.18	.45
Ryan	.69	.26	.43	.31	.58
North Twin	.71[1]	.16	.55[1]	.29	.65[1]
Marl	.80	.36	.44	.20	.69
Doyle	.84	.27	.57	.16	.78

[1] Includes 100 trout estimated mortality from oxygen depletion

$N = a + s = 1.00$

$a = u + v, \; s = 1 - a$

$\frac{v}{v+s} = \frac{v}{N-u}$ or: ratio of natural mortality to population excluding fish removed by fishing.

between lakes. A better comparison of natural mortality between lakes is the ratio of loss from natural deaths to the population excluding trout removed by fishing.

To explain this ratio, the total trout population (N) can be equated in terms of mortality and survival as:

$$N = a + s \qquad \text{or} \qquad N = u + v + s$$

In this equation as fishing mortality (u) becomes greater, less fish are available to die from natural causes. Therefore if N is equated to one, as fishing mortality (u) approaches one, natural mortality (v) approaches zero, and survival (s) approaches zero. Thus the fraction of natural mortality based on the whole population is not valid for comparison between lakes unless fishing mortality is constant. The best comparison between lakes is to consider the fraction of natural mortality of the population remaining after fishing mortality has been excluded $\frac{v}{v + s}$.

Quality of angling

The selection of experimental lakes on private lands where trespass was controlled allowed an adequate and economical creel census. Each fisherman was required to obtain a creel census card from the landowner before going fishing. At the completion of each fishing trip the angler recorded 1) the length in inches of each fish caught and retained or released; 2) the approximate depth at which fish were taken; and 3) a record of the number of hours fished. Each card was then returned to the landowner.

The creel census cards were collected on every visit to the lakes by the investigator. This provided an opportunity for discussion of fishing conditions, and checking on any irregularities in the creel census procedure of which the landowner had personal knowledge. Measuring boards were provided at each lake marked in tenths of inches. This apparently confused many of the fishermen who persisted in recording the fish lengths in eighths of inches. The reported fish lengths were not used in growth calculations.

A total of 1,457 of the 8,545 trout planted were reported in the creel census. No fishing by anglers was permitted on Norway, South Twin, and North Twin lakes at the request of the landowners. Fishing was permitted on the remaining seven lakes, except that Little Headquarters Lake was closed to fishing on August 30 to insure a sufficiently large population for growth collections during the remainder of the season. Little Lake was fished very little because it was a remote lake, reached only after traveling a long, rough road.

As can be expected in a census of this kind not all anglers filled the reports out correctly. The major effort made in checking cards was to insure that all fish caught were reported at least in number. To calculate a catch-per-hour statistic, all incomplete cards were disregarded. On the complete cards 1,289 fish were reported taken in 1,366 hours of fishing, or a catch per hour of .94 trout. This figure may be somewhat high as some unsuccessful anglers may not have turned in a report. However, any such error is considered negligible. This catch per hour is high in comparison with similar trout lakes in the area because on these private lakes fishing pressure was comparatively very light.

Fishing success was essentially the same all season, with the exception of Slide, Doyle, and Little Headquarters lakes where the catch per hour declined in August (Table 12). It was observed that a few expert fishermen influenced the catch per hour. These fishermen could take limit catches of 5 trout almost at will. The Doyle and Little Headquarters report of limit catches in Table 12 reflect the presence of these fishermen at the Mid-Forest Lodge.

Most of the anglers fished with bait; few of the anglers used artificial flies. Fish were taken principally from depths of 5 feet to 10 feet in May on all lakes, but as the season progressed fishermen reported increasing depth of capture in the deep lakes (Bass, Ryan, and Doyle).

Generally the fishermen were very pleased with the quality of fishing. No complaints of poor taste or poor appearance of the trout were reported.

Dynamics of the trout populations

Growth and mortality have each been discussed as parameters of trout success. The ten lakes have been evaluated on the criteria of rapid growth, and again on low natural mortality with respect to the trout populations. The concepts of exponential growth and mortality

Table 12. Monthly summary of fish taken by anglers, 1960[1]

Month	Little	Little Hdqrs.	Marl	Doyle	Slide	Bass	Ryan
				Number of fish			
April	--	--	--	--	--	--	--
May	--	97	2	124	77	1	45
June	2	21	58	61	85	34	126
July	3	34	--	240	60	10	43
August	--	71	--	43	26	27	16
September	--	--	--	--	--	26	22
October	--	--	--	--	--	103	--
Total	5	223	60	468	248	201	252
				Catch per hour			
April	--	--	--	--	--	--	--
May	--	.90	.50	.78	1.53	.25	1.10
June	.33	.78	1.11	.71	1.41	1.41	1.09
July	.20	.92	--	1.31	1.14	.83	.84
August	--	.49	--	.36	.48	1.08	1.00
September	--	--	--	--	--	.94	1.22
October	--	--	--	--	--	1.23	--
Average	.27	.77	.81	.79	1.02	.96	1.05
				Number of limit catches			
April	--	--	--	--	--	--	--
May	--	9	0	15	12	0	5
June	0	1	9	8	13	5	16
July	0	2	--	40	7	1	4
August	--	7	--	1	3	1	3
September	--	--	--	--	--	2	3
October	--	--	--	--	--	12	--
Total	0	19	9	64	35	21	31
Percent of total catch	0.0	42.6	75.0	68.4	70.6	52.2	61.5

[1]Norway, South Twin, North Twin had no angling pressure.

developed by Clarke, et al. (1946) provide a basis for study of the interaction of these factors. On a space and time continuum, quantitative computation can be made of standing crop, production, mortality and survival.

In the ten trout populations of this study all of the fish were stocked. There was no natural reproduction or migration of wild trout into the lakes. Computation of the population dynamics requires, therefore, only the following vital statistics: 1) number and weight of trout at the start of the season (actual plants), 2) the rate of growth in weight during successive short periods of the season, and 3) the rate of mortality during the same periods (Ricker and Foerster, 1948).

The number and weight of the trout stocked are accurately known (see page 15, and Table 2, page 16). Only the legal trout are considered in these computations because the population of fingerling trout present in any lake, except Little Headquarters, was negligible throughout the season.

To compute growth and mortality rates the season was divided into five successive periods; each period was 5 weeks long. One-half of the legal trout were planted on April 20 and the other half 5 weeks later in May. The 5-week periods simplified the computations and eliminated introduction of error as the second period began with the second plant. Periodic growth collections of trout were made at 5- to 6-week intervals which coincided with the termination of each computation period. The final 5-week period terminated on October 8.

The standing crop and number of trout estimated present on October 9 was designated as the surviving population at the end of the season. The trout removed in the final gill-net and rotenone harvest operation are thus considered in these computations only indirectly as part of the final standing crop.

The mean weight of the individual trout (W_o) at the start and end (W_1) of each successive 5-week period was extrapolated directly from the synthetic growth curves. The instantaneous rate of growth (g) was computed from the equation:

$$\frac{W_1}{W_o} = e^{g}, \quad \text{and } g = \log_e (W_1 / W_o)$$

(cf. Ricker, 1958 for details of this and succeeding calculations. The actual computation was done by use of Ricker's Tables.)

In a similar manner the instantaneous rate of mortality (i) can be computed from the number of trout present at the start (N_o) and end (N_1), of each period from the following equation:

$$\frac{N_1}{N_o} = e^{-i} \quad \text{or, } i = -\log_e (1 - a)$$

where a = fraction of fish that die during period.

However, the date of death was unknown for 38 percent of the trout of the ten populations. It is assumed that the rate of this unknown mortality was exponential. Therefore, the number of trout present at the beginning and end of each 5-week interval was approximated by the following procedure for each lake. The entire season (April 20 through the rotenone kill in late October in this instance) was further subdivided into successive weekly intervals. The known mortality (average 62%) was posted by date into the weekly period of occurrence. The instantaneous rate of mortality for the entire season was then computed for the remaining fish. The number of fish expected to die (natural mortality) in the first week was then computed and subtracted from the total population. This procedure was repeated for each successive week of the season in conjunction with the known mortality until at the end of the final week the population was equal to zero. I then computed the instantaneous rate of mortality for the total population by 5-week periods corresponding to the same periods for the instantaneous rate of growth.

As the fraction of fishing mortality (angler catch and growth collections combined) was known the instantaneous rate of fishing mortality (p) and the instantaneous rate of natural mortality (q) were also computed from the following relationship:

$$i = p + q$$

The data is now at hand to compute the mean standing crop ($\overline{W}$) for each interval. Mean standing crop is computed from the relationship:

$$\overline{W} = \frac{W(e^{g-i} - 1)}{g - i}$$

When W equals the standing crop at the beginning of the interval, $\overline{W}$ is computed simply by multiplying the number of fish present at the start of the interval by their mean weight. All computations up to this point were made on the basis of fish weight in grams. I transformed $\overline{W}$

from grams of fish per lake to a unit of pounds/acre by:

$$\frac{\bar{W}}{(454)\ (\text{lake size (A)})}$$

The mean standing crop can be multiplied by any instantaneous rate to determine the mass (total weight) of fish involved for the period. These computations were made for each population:

$\underline{g}\bar{W}$ = production, total growth in weight of fish for the interval including the growth made by fish that died during the interval

$\underline{i}\bar{W}$ = total mortality

$\underline{p}\bar{W}$ = fishing mortality

$\underline{q}\bar{W}$ = natural mortality, or mortality from all other causes than fishing

The population dynamics of Slide Lake are shown graphically in Figure 17. In this graph the mean weight of individual trout, population size (number of fish), and mean standing crop are plotted for weekly intervals throughout the season. Production and mortality are shown for corresponding 5-week intervals. Five hundred and fifty legal trout were planted on April 20. During the ensuing 5 weeks production exceeded total mortality and the standing crop rose steadily. This was true because the growth rate was rapid, and both fishing and natural mortality were low. On May 20 the second plant of 510 legal trout was made. The impact of this plant was to nearly double the number of trout in the population and also the standing crop. As the mean size of the trout in the

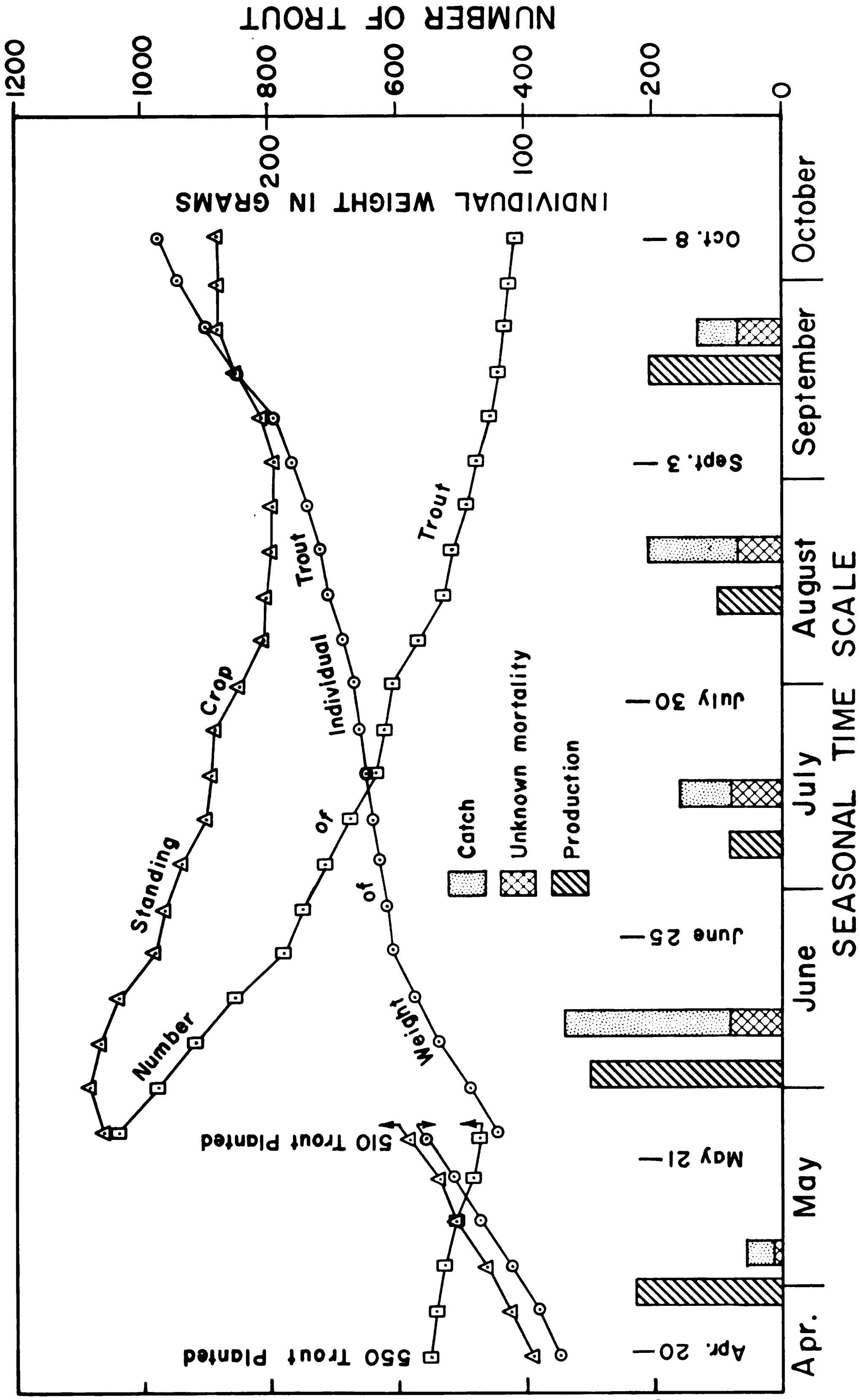


Fig. 17. Slide Lake--population dynamics, 1960.

second plant was smaller than the survivors of the first plant, the mean size of the individual trout dropped slightly.

Slide Lake was opened to angling on June 1. The combined fishermen catch, gill-net collections, and natural mortality steadily depleted the numbers of trout in the population throughout the remainder of the season. The growth rate of the trout was rapid in June, declined in July and August, but increased again in September. Consequently, production exceeded mortality only in early June and again in September during which periods the standing crop increased. The rate of decrease in standing crop during July and August was proportionately less than the decrease in trout numbers because some growth accrued during these months. The final standing crop on October 8 was 21.4 pounds per acre, a biomass slightly greater than the 20.8 pounds per acre originally planted in April and May. This was the direct result of a production of 23.0 pounds per acre which exceeded the total mortality of 22.3 pounds per acre. The mean standing crop was 20.2 pounds per acre, only slightly less than the 20.8 pounds per acre originally stocked.

To judge this population from the viewpoint of providing fish for the angler to catch, it is necessary to consider total available stock and mortality other than fishing. Slide Lake had a total available trout stock of 43.7 pounds per acre derived from the 20.8 pounds per acre planted and the 23.0 pounds per acre produced. Of this available stock, only 8.2 pounds per acre were lost to natural mortality. Harvest, or fishing mortality, took 14.1 pounds per acre leaving 21.4 pounds per acre at the end of the season. This private lake was not fished intensively. If the fishing pressure had been greater, a higher proportion of the available stock would have gone into the harvest. In this event production would have dropped almost in proportion to the increase in the rate of instantaneous mortality, because any additional growth would have been minor. This conclusion is based on the hypothesis that growth was regulated in this population more by temperature than by population densities.

Slide Lake has been portrayed graphically only to illustrate the relationship of the dynamics of one population throughout the season. In Table 13 a comparison is made of population statistics among the ten lakes. A quantitative comparison of the source of the available stock and its dispersal into fishing mortality, natural mortality and final standing crop is shown in Figure 18 for each of the ten lakes.

Table 13 affords a comparison of the total production of trout among lakes. However, if the populations are compared simply on the basis of total production the result is heavily biased by the planting rate which varied between lakes. Little Lake and Marl Lake had low planting rates and, consequently, low standing crops and production even though the growth rates were relatively high. Planting rate is an important variable influencing production.

A comparison of production between lakes can be made by taking the ratio of production to weight of the trout stocked. This

Table 13. Summary of plant, production, mortality and mean standing crop for each trout population in 1960

(All data except number of trout planted expressed in pounds per acre)

Lake	Legal trout plant		Production (2)	Available stock (1 + 2)	Fishing mortality (3)	Natural mortality (4)	Total mortality (3 + 4)	Final standing crop (Oct. 8)	Mean standing crop (season)
	Number per acre	Weight (1)							
Little	42	8.46	11.45	19.91	5.60	2.35	7.95	11.96	11.41
Little Hdqrs.	88	17.17	16.02	33.19	19.19	4.44	23.63	9.56	12.07
Doyle	101	19.96	15.58	35.54	8.49	18.34	26.83	8.71	12.65
Marl	62	12.24	10.26	22.50	6.84	8.56	15.40	7.10	8.58
Slide	106	20.78	22.96	43.74	14.08	8.24	22.32	21.42	20.18
North Twin	99	19.67	18.91	38.58	5.53	17.38	22.91	15.67	15.70
Bass	97	19.02	22.93	41.95	18.32	3.92	22.24	19.71	23.20
Norway	103	20.27	12.11	32.38	9.10	7.73	16.83	15.55	16.91
South Twin	115	22.43	12.37	34.80	9.88	3.99	13.87	20.93	21.58
Ryan	101	19.73	5.99	25.72	6.70	10.76	17.46	8.26	13.08
Mean value	91.4	17.97	14.86	32.83	10.37	8.57	18.94	13.89	15.54

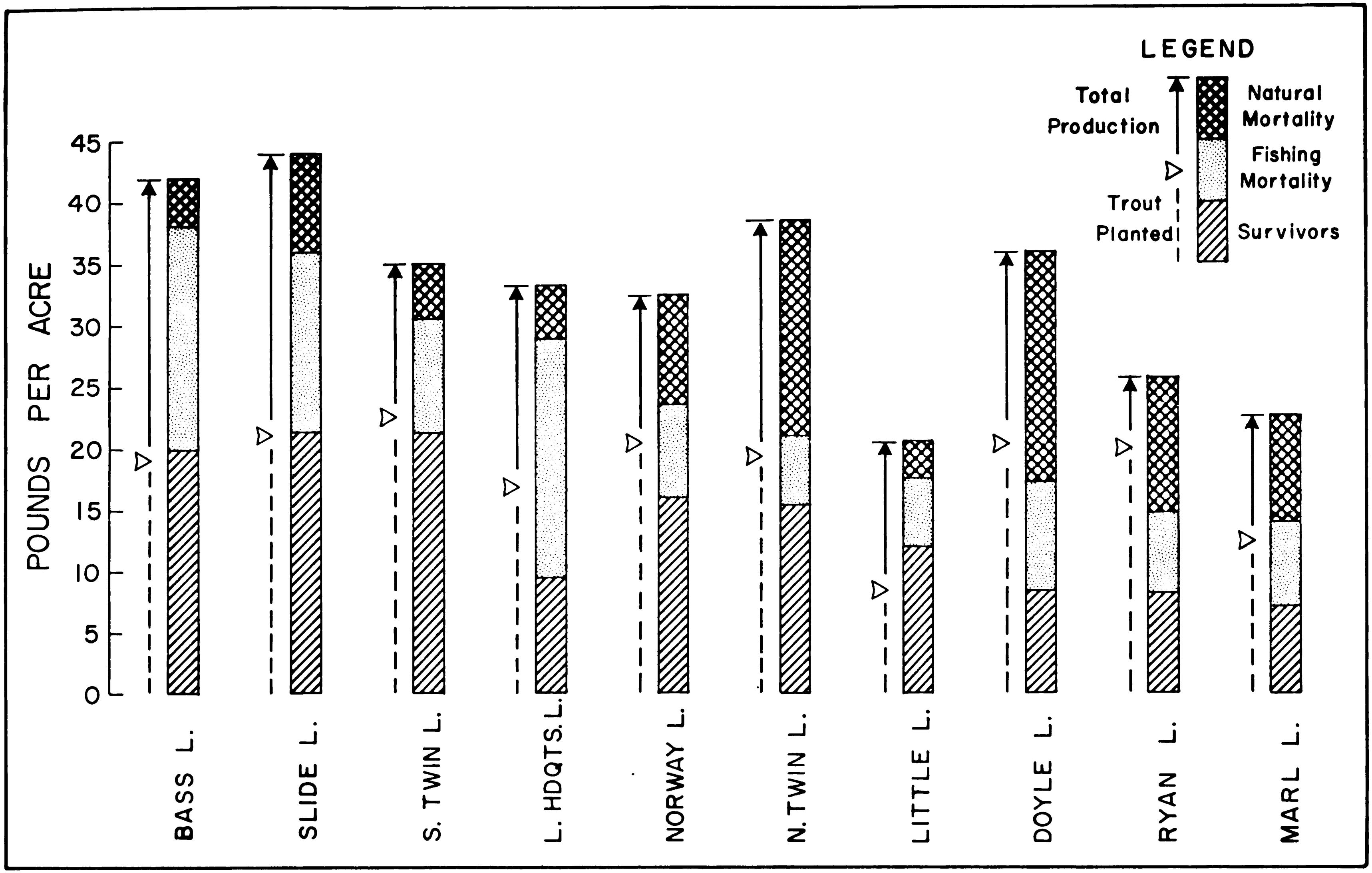


Fig. 18. Diagram of the available trout stock in each of the ten lakes, 1960.

ratio eliminates the bias of differing planting rates. In this case production may be influenced by the effect of population density on the rate of growth. Population density, or mean standing crop, is considered an environmental factor and will be discussed later.

In Figure 18 an interesting characteristic of the net result of the population dynamics is illustrated. The weight of the stock planted combined additively with production constitutes the total available stock of trout for the season. Natural mortality, however, limits the stock available for the fishermen. A valid measure of the stock available for the fishery can be made by combining the weight of fish caught (Y) with the remaining standing crop (W_t). A measure of the efficiency of the population in providing a fishing stock can be derived by dividing this quantity by the original stock (weight) of fish planted W_o . This percentage or efficiency index can be stated more simply as:

$$\frac{\text{total fishing mortality + remaining standing crop}}{\text{fish stocked}}$$

or Efficiency Index $= \frac{Y + W_t}{W_o}$ which can be computed at any point of time during the existence of the population.

At the immediate time of planting the index would equal 1.00 (100%) as the standing crop would exactly equal the weight planted and fishing mortality would be 0.00. Any time during the existence of the stock the index could be greater or less than 1.00 depending upon the quantity of fish taken and the remaining standing crop. An index of 3.00 at any given time, for example, would show that three times the weight of fish planted had either been taken or remained to be caught. A value of 0.50 would show that only one-half of the weight stocked had been taken or remained to be caught. When at some future time mortality was complete and standing crop was equal to 0.00 the index would give the percentage returns to the fishery of the weight originally stocked.

If in this study the fish taken in growth collections and fish taken by anglers are combined the relative efficiency of each population in providing a stock of fish for the fishery can be computed.[5] Results of this computation are presented in Table 14.

---

[5]It is assumed that fishing mortality for the rainbow trout in these lakes is proportional to fishing intensity regardless of the gear employed.

In Little Headquarters Lake 19.0 pounds per acre of trout were taken by fishing which was greater than the 17.2 pounds per acre planted. This was the only population wherein fishing mortality exceeded the quantity of trout stocked. Little Headquarters Lake on the Mid-Forest Lodge property is the site of a residential area and, consequently, was fished to a greater degree by anglers than any of the other lakes. I removed trout from Little Headquarters Lake by gill-net collection in proportionate numbers to the other lakes. On July 30, I realized that fishermen had removed some 223 fish out of the original plant of 540, or nearly half of the entire stock. At this point I became concerned with the fact that the population would become so depleted in numbers that growth collections would be difficult to obtain later in the season. I therefore requested the Mid-Forest Lodge president to close the lake to fishing. None of the other lakes were subjected to intensive fishing and such action was not necessary.

Based on this experience on Little Headquarters Lake I assume that a similar or greater number of the trout removed in the gill net growth collections would have been taken by fishermen had the angling pressure been proportionately higher.

Table 14. Computation of relative efficiency index. Rainbow trout populations, 1960

(Values in pounds per acre)

Lake	Fishing mortality (Y)	Final standing crop (W_f)	$(Y + W_f)$	Plant (W_o)	Relative efficiency $\frac{Y + W_f}{W_o}$
Little	5.60	11.96	17.56	8.46	2.07
Bass	18.32	19.71	38.03	19.02	2.00
Slide	14.08	21.42	35.50	20.78	1.71
Little Hdqrs.	19.19	9.56	28.75	17.17	1.67
South Twin	9.88	20.93	30.81	22.43	1.37
Norway	9.10	15.55	24.65	20.27	1.22
Marl	6.84	7.10	13.94	12.24	1.14
North Twin	5.53	15.67	21.20	19.67	1.08
Doyle	8.49	8.71	17.20	19.96	.86
Ryan	6.70	8.26	14.96	19.73	.76

Environmental Conditions

At 2-week intervals throughout the 1960 season each lake was investigated to obtain information on the existing environmental conditions. Data were collected on temperature, dissolved oxygen, phenolphthalein and methyl orange alkalinity, free carbon dioxide, pH and transparency. At each of these visits observations were made on trout, predatory animal and human activity. In mid-summer each lake basin was mapped with a sonic sounder, and records were made of the lake bottom soil types, species and abundance of aquatic plants, and the character of the shoreline and surrounding upland features. Occasional night observations were made with electric lights and direct current electrofishing gear on Bass, Slide, Marl, Little and Little Headquarters lakes.

Morphometry

The shoreline configuration of each lake was scaled from U. S. Department of Agriculture aerial photographs to provide base maps for field investigations. Seasonal variation in water levels caused some errors in the base maps which were checked and corrected to mid-summer conditions. Several radial transects were run on each lake with a sonic sounder to determine water depths. Bottom depth contours at 1-meter intervals were mapped by interpolation of the sonic transects. The lake surface area and the area contained by each depth contour were measured with a polar planimeter. The surface area and depth of each lake are summarized in Table 16, and a map of the ten lake basins is shown in Figure 3.

In Table 15 a summary is given of the accumulative area of bottom at depth intervals of one meter, and for comparisons among lakes these areas are expressed in percent of the lake bottom.

Lake bottom soils

At the time of mapping, the bottom soil types were determined by direct observation in the shallow, littoral areas; and by sampling with an Ekman dredge in deeper areas. The bottom soils are described after the classification of Roelofs (1944). A short description of the bottom soils follows for each of the lakes.

Marl Lake.--White sand along shore, overlaid in deeper waters with up to 24 inches of green-brown, pulpy peat. There are some marl deposits.

Little Headquarters Lake.--White sand along shore grading into marl; some thin deposits of pulpy peat overlaying gravel at maximum depths.

Slide Lake.--Bottom soils are the same as Little Headquarters except more extensive deposits of marl.

Little Lake.--The bottom of the littoral zone is a brown, fibrous peat. In deep water areas the bottom is a green-brown, pulpy peat covered with a dense aquatic moss.

Ryan Lake, *Doyle Lake*.--Entire bottom is brown and black pulpy peat and muck.

Table 15. Accumulative percentage of lake bottom at each depth contour

Depth (meters)	Bass	Doyle	South Twin	North Twin	Ryan	Norway	Little	Slide	Little Hdqrs.	Marl
1	13.0	38.2	13.0	14.8	20.4	9.7	28.6	37.5	38.6	63.2
2	22.9	72.2	22.6	26.4	30.5	20.5	39.2	67.5	64.1	83.7
3	28.0	77.6	28.3	38.7	37.6	30.0	77.5	86.8	84.2	99.1
4	35.4	81.5	41.9	51.4	49.7	51.7	93.2	94.3	100.0	100.0
5	41.3	86.3	54.8	61.8	58.3	72.9	99.7	99.3		
6	53.8	90.0	64.8	74.4	76.3	100.0	100.0	100.0		
7	64.2	94.6	79.4	83.2	100.0					
8	72.9	98.0	89.7	90.9						
9	80.3	99.3	100.0	100.0						
10	87.4	100.0								
11	91.6									
12	96.2									
13	98.6									
14	99.7									
15	100.0									

- - - - - lower limit of 3.0 ppm dissolved oxygen.

——— lower limit of 0.0+ ppm dissolved oxygen.

Bass Lake. --Entire bottom pulpy peat and muck. In profundal zone black, pulpy peat with strong odor of hydrogen sulphide.

Norway Lake. --Bottom near shore a brown fibrous peat; in deeper water it grades into a black, pulpy peat. Entire bottom is littered with undecomposed leaves and sticks.

South Twin and North Twin lakes. --Entire bottom is a black, pulpy peat or muck.

Aquatic plants

Samples of the dominant aquatic plants were collected when the lakes were mapped. Plankton samples were taken only in Norway and North Twin lakes where algae blooms were evident. The more conspicuous aquatic plants are summarized here, briefly, for each lake.

Marl Lake. --Aquatic plants are very scarce. There are a few scattered plants of *Najas* and *Potamogeton* and one large *Chara* bed.

Little Headquarters Lake. --Extensive *Chara* beds throughout the lake. *Najas* is fairly abundant and there are some scattered plants of *Nuphar*, *Scirpus*, *Potamogeton natans*, and *P. amplifolius*.

Slide Lake. --Extensive *Chara* beds. Very few higher aquatic plants. In late summer many *Chara* beds rise from the bottom and turn yellow, causing an unsightly appearance to the lake.

Little Lake. --*Nuphar*, *Nymphaea*, and *Brasenia* are found in a zone 50 feet wide around the entire lake margin. Submerged aquatics are fairly abundant in the littoral zone consisting of *P. amplifolius* and *Utricularia*.

Ryan Lake.--A dense bed of Nuphar and Numphaea surrounds the lake along the shoreline. Dense growths of Ranunculus and Potamogeton occur down to depths of 10 feet all around the basin.

Doyle Lake.--This lake has the most abundant growth of higher aquatic plants of any of the ten lakes. Nuphar grows over about two thirds of the lake area. In the shallow areas dense beds of Chara and Najas are found. In depths of from 5 to 15 feet many Potamogetons especially P. zosteriformis occur, succeeded in still deeper water by beds of Nitella.

Bass Lake.--A narrow band of Nuphar and Nymphaea around shore. Some beds of Potamogeton border the water lilies. Chara beds border the Potamogetons and extend down to depths of 7 to 10 feet. No plants were found at greater depths.

Norway Lake.--No higher plants or Characeae were found. The deep-green water color which lasts throughout the season is believed due to a colloidal clay, and a continuous bloom of blue-green algae of which Microcystis and Anabaena were most common.

South Twin Lake.--A rim of Pontederia, Nuphar, and Nymphaea extends out about 25 feet from shore around the precipitous basin. This is flanked by Ceratophyllum beds down to 10 feet in depth. A few other Potamogeton, Myriophyllum, Elodea, and Utricularia specimens were intermixed. No plants were found below 10 feet in depth.

North Twin Lake.--A rim of Nuphar and Nymphaea extends around the lake. This is flanked by Ceratophyllum and P. pectinatus beds which extend to a depth of about 5 feet. No other submerged aquatic plants were found, but scums of algae and Lemna were common. Frequent algae blooms occur in this lake; Coelosphaerium and Anabaena were common.

Connecting waters

Marl, Little Headquarters, Slide, Little and Norway lakes are completely landlocked lakes. None of them have outlets, but Little Headquarters Lake is fed by a flowing spring. Little Lake has a small intermittent inlet containing a small beaver pond.

Doyle Lake is also a landlocked lake. Its outlet seeps away, several hundred yards below the lake, into the porous sandy soil of the area. Doyle Lake does have a small inlet, and the lake level is maintained at present by an old beaver dam.

The remaining four lakes are connected to other surface waters in their drainage systems by permanent inlets and outlets. The outlet of Ryan Lake constitutes the source of Denton Creek. Bass Lake drains through a cedar swamp area to the Tobacco River, and North and South Twin lakes are on a small tributary stream of the Muskegon River.

Barrier dams were installed on these lakes to prevent the entry of non-trout species after the rotenone treatment. Inclined screen structures were used at North Twin and South Twin lakes, and outlet screens on the culverts below Ryan and Bass lakes. These devices were not entirely effective as non-trout species were reestablished in all four lakes. Minnows (redbelly dace) were also found in Doyle Lake after the rotenone treatment. No non-trout species were found in Marl, Little, Little Headquarters and Norway lakes after chemical treatment. Slide Lake had no existing fish population in 1959 when it was selected for this experiment.

Chemical and thermal water characteristics

To standardize the collection of water analysis data, one permanent station was established at the deepest point in each lake. This station was marked with a buoy which afforded an anchorage point for the survey boat. Water samples were collected with a modified Kemmerer sampler at one-meter intervals from the surface to the bottom to establish temperature and chemical water profiles. As the lakes were small (3 to 23 acres) it was assumed that one profile (located at buoy) would give a reliable measurement for the entire lake. Temperature and Secchi disc readings were recorded directly at the sampling station. Water samples for dissolved oxygen and alkalinity determination were taken ashore and processed in a portable field laboratory (Fig. 19).

Water temperatures were taken with a Whitney electric resistance thermometer. Some doubts were held as to the accuracy of this device; consequently, it was checked periodically with a standard mercury thermometer and calibrated in the laboratory. An occasional water sample was checked in the field against a reliable pocket thermometer. The temperature data are considered accurate to within ±1 F.

A complete description of the water temperatures by depths throughout the season is furnished in figures in Appendix B for each lake. Temperature stratification is indicated by connecting lines of

Fig. 19. Portable field chemistry laboratory.

Fig. 20. Method of handling water samples in bulk for field chemical analysis. Kit is for fixing oxygen samples.

like temperature at 5- degree intervals on a seasonal time scale. In addition, temperature profiles for one measurement in the spring shortly after ice-out, and one measurement in the summer at the time of maximum stratification are furnished in Appendix B for each lake.

Dissolved oxygen was determined by the Alsterberg (Azide) Modification of the Winkler Method. Occasional samples were checked for iron interference with potassium fluoride reagent. No erroneous results were detected. A complete record of oxygen stratification is included in the Appendix to correspond with the temperature records. In Table 15, the lower limit of dissolved oxygen is indicated by depth.

Phenolphthalein and methyl orange alkalinities and free carbon dioxide were determined by the methods outlined in Standard Methods for Examination of Water and Sewage (1960). A Beckman pocket pH meter and at times a Hellige colorimeter were used to determine the hydrogen ion concentration. Some difficulty was met in the determination of free carbon dioxide in the stagnant waters of the deeper lakes probably due to the interference of organic acids.

Profiles are given in Appendix B for phenolphthalein and methyl orange alkalinity, free carbon dioxide, and hydrogen ion content both in early April and mid-August. Water transparency readings were taken with a standard Secchi disc on the shaded side of the survey boat.

Total alkalinity as the mean of the successive values determined throughout the season are summarized for surface and bottom waters in Table 16. Phenothalein alkalinity is summarized separately as the maximum value determined at a depth of one meter throughout the season. The range in transparency and the mean value are also summarized in Table 16. In three of the lakes--Marl, Little Headquarters and Slide, the bottom was visible even at maximum depths throughout the season.

The basin slope of each lake based on the accumulative percentage of area by depth is shown graphically in Figure 21. The mid-summer dissolved oxygen stratification is shaded in each of the figures at intervals of 5.0 ppm and 0.0 ppm. The surface temperature, thermocline, and bottom temperatures are also provided. This diagram shows the depth and extent of the profundal areas in the deeper lakes in contrast with the shallow, unstratified lakes.

Bass Lake has dissolved oxygen (less than 3.0 ppm) below the thermocline. In North Twin, the lake polluted with organic wastes, dissolved oxygen declines to 0.0 midway through the thermocline. In all the other stratified lakes the 0.0 ppm dissolved oxygen level coincides very closely with the lower limit of the thermocline. Neither Bass Lake or North Twin Lake underwent a complete overturn in the spring of 1960.

Population density and competition

The fish populations of all ten lakes were eradicated in October, 1959 with rotenone, but four of the lakes were re-populated to some extent with non-trout species before the trout were planted the

Table 16. Summary of area, depth, alkalinity and transparency characteristics of the ten experimental lakes in 1960

Lake	Area (acres)	Maximum depth (meters)	Average depth (meters)	Total methyl-orange alkalinity (seasonal average)		Maximum ph-th alkalinity (1 meter) (ppm)	Transparency (depth in feet)	
				Surface (ppm)	Bottom (ppm)		Range	Average
Little	6.5	5.1	2.1	20	38	0	5-10	7
Little Hdqrs.	6.2	3.1	1.6	60	60	12	bottom (11')	
Doyle	23.0	9.0	2.1	70	78	7	10-15	13
Marl	11.8	3.0	1.0	45	45	7	bottom (10')	
Slide	10.0	5.0	1.6	82	82	17	bottom (15')	
North Twin	3.6	8.2	4.1	140	315	25	2-10	4
Bass	6.9	14.0	5.7	100	140	7	9-17	13
Norway	4.4	5.2	3.5	16	25	5	2-3	2.5
South Twin	3.0	8.8	4.8	135	216	8	5-10	7
Ryan	14.7	6.4	3.6	70	60	0	6-11	7

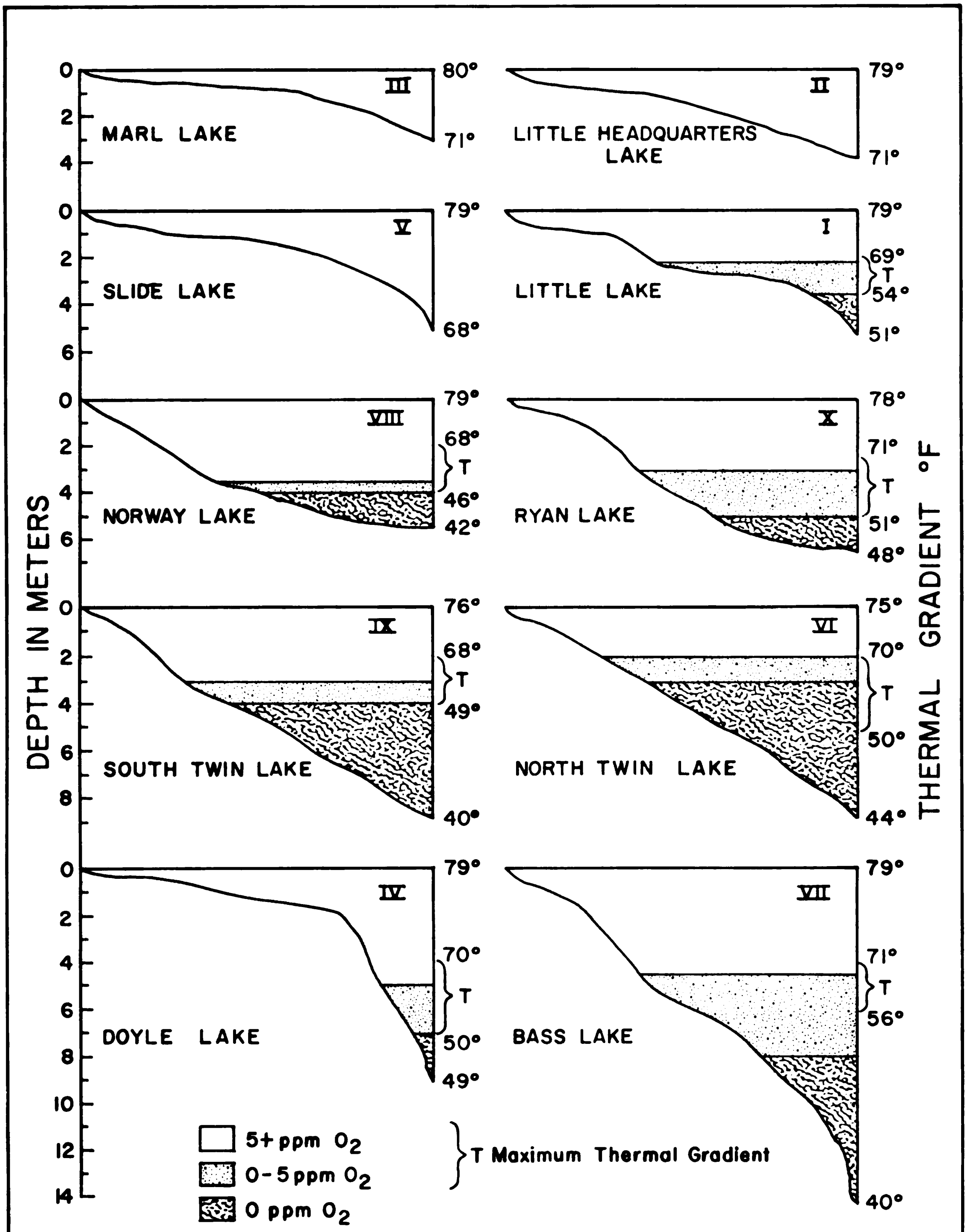


Fig. 21. Basin slope, dissolved oxygen content, and thermal stratification of the experimental lakes during period of maximum temperatures in summer, 1960. Horizontal axis represents lake surface area on a percentage basis.

following April. These four lakes were Ryan, Bass, North Twin and South Twin. A few redbelly dace were found in Doyle Lake. In Little Headquarters, Marl, Little, Slide, and Norway lakes the 1960 fish populations consisted only of trout.

Estimates of the mean standing crop of trout in each lake are available from the computation of population dynamics. These data (for legal trout) are summarized for the season by successive 5-week periods in Table 17. The plant of fingerlings on May 24, 1960, consisted of approximately 0.25 pounds per acre in each lake. Only in Little Headquarters Lake did the fingerling population build up a sufficiently large biomass to be quantitatively measured during the season. In Little Headquarters Lake the final standing crop of fingerling trout was estimated at 5.0 pounds per acre on October 20. The mean standing crop for the entire season can be estimated as approximately 2.6 pounds per acre.

The non-trout fish species found in the October 20, 1960, rotenone treatment of Bass, Ryan, North Twin and South Twin lakes are listed in Table 18. The species are arranged in approximate descending order according to their relative abundance by weight.

The mark-and-release method of estimation used for the trout populations could not be applied to the non-trout species. It was impossible during the rotenone kill to pick up numbers of the non-trout species proportional to the recovery of trout, as they did not surface and die at the same rate as trout. Some fish, like bluegill and crappie

Table 17. Mean standing crop of trout (pounds per acre) for consecutive five-week periods in 1960

Lake	Weight of plant (Pounds per acre)	Mean standing crop					Final standing crop (Oct. 8)	Mean standing crop (season)
		April 20 - May 21	May 22 - June 25	June 26 - July 30	July 31 - Sept. 3	Sept. 4 - Oct. 8		
Little	8.46	--	9.95	12.23	12.01	11.45	11.99	11.41
Little Hdqrs.	17.17	9.26	16.24	14.81	11.11	8.95	9.35	12.07
Doyle	19.96	9.59	18.25	14.88	11.20	9.32	8.49	12.65
Marl	12.24	6.67	12.10	9.84	7.46	6.81	7.14	8.58
Slide	20.78	12.61	24.22	22.98	20.67	20.42	21.36	20.18
North Twin	19.67	12.80	20.53	17.19	14.17	13.80	15.39	15.70
Bass	19.02	10.42	23.89	29.26	29.17	23.28	19.27	23.20
Norway	20.27	11.01	20.47	20.10	17.58	15.37	15.13	16.91
South Twin	22.43	13.83	25.99	24.78	22.03	21.25	20.64	21.58
Ryan	19.73	9.76	18.63	15.57	12.06	9.40	8.15	13.08

Table 18. Fishes other than rainbow trout collected in 1960 from the experimental lakes.[1] [2] List is in order of relative abundance by weight.

Ryan Lake	North Twin Lake	South Twin Lake	Bass Lake
Bullheads[3]	Largemouth bass	Bullheads	Bluegill
Golden shiner	Common shiner	Bluegill	Redbelly dace
Yellow perch	Bullheads	Largemouth bass	Creek chub
Northern pike	White sucker	Pumpkinseed	Stickleback
Pumpkinseed	Golden shiner	Creek chub	Pumpkinseed
Redbelly dace	Bluegill	Yellow perch	Largemouth bass
Mudminnow	Pumpkinseed	Golden shiner	Green sunfish
	Creek chub	Northern pike (1)	Yellow perch
	Yellow perch	Redbelly dace	Common shiner
	Black crappie	Mudminnow	Johnny darter
	Shiner (Unident.)		

[1] A few redbelly dace were collected in Doyle Lake.

[2] Complete list of full common name and scientific name of fishes is provided in Appendix.

[3] Brown, black, and yellow bullheads are combined; all three species were found but the relative abundance or specific occurrence was not recorded for each lake.

fingerlings, appeared quickly after the treatment, while other species such as bullheads did not appear for several hours.

A large, composite sample of the non-trout species was collected during the period of distress from rotenone poisoning. All fish in this sample were separated by species, counted, and weighed to determine their relative abundance.

No accurate estimate of the biomass of non-trout species could be made. I concluded, simply, that the biomass of non-trout species was considerably greater in all four of these lakes than the biomass of the trout present, and that the biomass of non-trout species (pounds per acre) was the largest in Ryan Lake, followed by North Twin, South Twin and Bass lakes in descending order of magnitude.

The proportion of adult fish to young-of-year fish varied in each of these lakes. In all four lakes adult fish had the best opportunity to migrate into the lake before the April plant of trout was made. In April the barrier screens were improved and I believe they were quite effective for the remainder of the season. If some adult fish survived the rotenone treatment they would have been present before April as well. Therefore, the proportion of adult fish in each lake population provides an indication of the biomass of each non-trout population during the season.

Many adult yellow perch, northern pike, and bullheads were found in Ryan Lake. North Twin Lake contained a smaller proportion of adult fish in the population than Ryan but more than either South

Twin or Bass lakes. The dominant species of adult fish in North Twin Lake were the white sucker, common shiner, golden shiner and bullheads (black, brown, and yellow). South Twin Lake had numerous adult yellow bullheads but very few adults of the other species. Bass Lake contained only a few adults of each species. From this information, I conclude that Ryan and North Twin lakes contained a larger biomass of non-trout species throughout the season than did South Twin and Bass lakes. In Bass Lake in particular, the total bulk of non-trout species was apparently very minor until the occurrence of a large bluegill hatch in June, after which time the total bulk increased very rapidly. In South Twin a considerable fraction of the non-trout population was young-of-the-year yellow perch. As this species spawns earlier than the bluegill, it can be assumed that the non-trout population in South Twin Lake built up somewhat earlier in the season than in Bass Lake.

In summary, the total biomass of the non-trout species was the greatest in Ryan Lake throughout the April to October 1960 season, followed by North Twin, South Twin and Bass lakes in successive order of magnitude.

Trout activity by water depth

The rainbow trout were found in the littoral areas of all ten lakes throughout the season. Trout were observed jumping or feeding at the surface on nearly all occasions when the lakes were visited--even in the months of July and August. Inhabitation of the littoral zone was evident from the locations at which rainbow trout were taken in gill nets throughout the season.

In all growth collections the depth at each end of the gill net was measured before pulling the net and removing the trout. Each gill net had a 6-foot depth of webbing. The location of each trout caught was marked on a simple diagram of the net-set to determine depth of capture. The recorded depths of trout capture for each lake are summarized in Table 19. All trout were caught in depths of 13 feet or less. Efforts were made to catch trout with gill nets in the deep water of Ryan, Bass, Doyle, and South Twin lakes, but the deep sets were never successful. No trout were taken in the gill nets in May from South Twin Lake, apparently the nets were set at depths below the trout population at the time. The littoral zone of South Twin Lake is only a narrow zone around the lake due to the sharp drop-off about 25 feet from shore. When the gill nets were set in the shallow littoral zone in later collections, trout were taken readily.

Overnight gill-net sets were successful while daytime sets took very few fish. However, it was noted on several occasions that the trout had been freshly gilled when the nets were checked in the early morning hours. It is probable that the trout are crepuscular, i.e., most active in the twilight and dawn periods.

Based on these observations it appears that the trout were well acclimated to the upper waters of each lake. However, there is some indication that the trout populations did shift into slightly deeper water .

Table 19. Number of trout caught at 1-foot intervals of depth in gill nets, 1960

Depth (feet)	Lake									
	Bass	Doyle	South Twin	North Twin	Ryan	Nor-way	Little	Slide	Little Hdqrs.	Marl
1	4	21	12	10	17	0	3	12	4	17
2	3	14	14	9	5	1	8	5	10	5
3	6	13	12	5	7	13	18	3	19	5
4	8	18	2	1	7	12	3	4	18	8
5	13	22	34	0	11	13	6	10	18	25
6	14	14	23	1	11	19	9	19	10	26
7	8	8	3	5	16	28	14	8	3	--
8	18	11	0	2	14	25	7	3	9	--
9	20	5	2	--	10	8	5	--	2	--
10	18	2	--	--	7	2	4	--	--	--
11	14	1	--	--	2	2	--	--	--	--
12	7	2	--	--	0	--	--	--	--	--
13	4	1	--	--	1	--	--	--	--	--
14	--	--	--	--	--	--	--	--	--	--
15	--	--	--	--	--	--	--	--	--	--
16	--	--	--	--	--	--	--	--	--	--
17	--	--	--	--	--	--	--	--	--	--
18	--	--	--	--	--	--	--	--	--	--
19	--	--	--	--	--	--	--	--	--	--
20	--	--	--	--	--	--	--	--	--	--
Total	137	132	102	33	108	123	77	64	93	86

in the deep, cool lakes with the advancing summer season, and then moved back into shallower water again in the fall (Table 20).

Table 20. Mean depth (feet) of trout capture at different seasons, 1960

Season	Lake		
	Bass	Doyle	Ryan
May	4.6	2.0	4.2
June	8.0	3.1	3.2
July	9.7	6.4	7.9
September	5.0	5.9	7.7

Food habits of rainbow trout

The availability of food organisms as an environmental factor influencing trout success was measured only indirectly in an analysis of trout food habits. Limitations of time precluded direct measurement of the invertebrate populations of each lake.

At each of four periodic trout collections (approximate dates: June 14, July 30, September 5, October 20) an analysis was made of trout stomach contents. This analysis was restricted to the legal trout, but no differentiation was made between the NC, A, and LP groups. Fish of varying sizes were selected and opened until ten stomachs containing food materials were found. Some of the collections, however, did not contain ten stomachs with food contents, and in these cases the analysis was conducted with the sample available. To avoid the necessity of stomach preservation and rehandling, the analysis was completed directly in the field. The contents of each stomach were spread in a shallow container. Each organism, or food material, was successively identified and the following information was recorded: 1) the number of stomachs containing each different organism, 2) the estimated percent, by volume, that the organism comprised of the total contents of all stomachs, and 3) an estimate of the total number of individuals of each organism for all stomachs.

A summary of the percent of stomachs containing various groups of food items is presented in Table 21. From this summary it can be concluded that bottom organisms were most frequently taken by the rainbow trout; organisms from the surface film were the next most frequent group; free-swimming organisms and aquatic plants were eaten less frequently, but were of considerable importance in certain lakes.

A large variety of food organisms was taken by the trout, but relatively few groups made up the bulk of the diet. Dragonfly nymphs stand out in importance. They constituted a major item of the diet in seven of the ten lakes. Diptera larvae, Hemiptera (Notonectidae and Corixidae), and small molluscs were important food items in most of the lakes. Chaoborus were important where they occurred in abundance (two lakes). The higher aquatic plant, Ceratophyllum constituted half the volume of the stomach contents in South Twin Lake.

Fig. 22. Field method of stomach analysis.

Table 21. Percentage of rainbow trout stomachs containing various food items. Figures in parentheses indicate number of stomachs with food items from each lake.

Food items	Little (34)	Little Hdqrs. (30)	Marl (34)	Doyle (30)	Slide (40)	North Twin (28)	Bass (30)	Norway (40)	South Twin (32)	Ryan (40)
Bottom organisms										
Odonata - Zygoptera (N)	35.3	70.0	67.6	90.0	77.5	--	36.7	7.5	6.3	37.5
Anisoptera (N)	38.2	20.0	29.4	20.0	17.5	35.7	--	--	3.1	--
Ephemeroptera (N)	--	30.0	35.3	23.3	25.0	10.7	--	--	3.1	--
Trichoptera (L)	4.1	6.7	--	--	5.0	--	--	15.0	6.3	10.0
Diptera-Chironomidae(L)	61.7	3.3	--	16.7	22.5	35.7	23.3	10.0	25.0	2.5
Other(L)	--	--	4.1	3.3	--	21.4	6.7	7.5	--	5.0
Mollusca	8.8	40.0	14.7	30.0	20.0	--	40.0	10.0	9.4	22.5
Malacostraca (Crayfish)	--	--	--	--	--	--	3.3	--	6.3	2.5
Free-swimming organisms										
Entromostra (Scuds)	4.1	3.3	5.9	--	11.4	14.3	--	11.4	9.4	--
Cladocera	20.6	--	--	--	--	53.6	3.3	2.5	50.0	2.5
Diptera - Chaoborous	52.9	--	--	3.3	--	--	--	62.5	43.8	5.0
Fish	--	--	--	--	--	10.7	30.0	--	3.1	--
Leeches	--	--	4.1	--	2.5	--	--	2.5	--	--
Surface organisms										
Hemiptera	64.7	33.3	35.3	20.0	25.0	21.4	26.7	55.0	6.3	40.0
Coleoptera-Aquatic A.	50.0	3.3	5.9	10.0	5.0	7.1	8.8	22.5	12.5	15.0
Terr. A.	4.1	6.7	5.9	6.7	5.0	10.7	--	2.5	6.3	15.0
Hymenoptera(Terr. A.)	5.9	6.7	8.8	6.7	10.0	--	--	--	--	25.0
Diptera A.	8.8	--	20.6	--	2.5	--	--	2.5	--	30.0
Aquatic plants										
Higher	--	3.3	--	10.0	5.0	7.1	23.3	--	56.3	22.5
Algae	--	13.4	8.8	10.0	5.0	10.7	6.7	7.5	6.3	5.0
Detritus	8.8	3.3	--	--	--	10.7	30.0	10.0	--	--

A summary of the four principal food items of the rainbow trout in each lake is presented in Table 22.

These findings agree with those of Hatch and Webster (1961) for rainbow trout food habits in the Adirondacks. Burdick and Cooper (1956) found also that rainbow trout in Weber Lake, Wisconsin, fed principally on bottom organisms. Leonard, et al., (1948) reported that bottom organisms comprised 40 percent of the diet of small (7" to 12") rainbows, but that 30 percent of the total diet was fish. I found that trout in three lakes ate fish but only the trout in Bass Lake ate fish (small minnows and centrarchids) in appreciable quantity. Small fish were eaten in Bass Lake during the late summer season when the K factor was decreasing and the trout were actually declining in weight. Johnson and Hasler (1954) state that rainbow trout feed almost exclusively on zooplankton from May through October in Wisconsin dystrophic lakes. No similar pattern existed in the lakes of this study, although Cladocera were important in the trout diet in three lakes.

Some trends in the seasonal change of diet were observed, but the number of stomachs analyzed was not large enough to draw rigid conclusions. In general, Chironomidae, *Chaoborus*, and other Diptera larvae occur in the stomachs in June and July. Dragonfly nymphs were taken all season but were less frequent in September and October. Corixidae, Notonectidae, small molluscs, fish, and aquatic plants were taken most frequently in the fall.

Table 22 Four principal food organisms of rainbow trout in each lake ranked by percent of volume of total stomach contents [1]

Lake	Rank or occurrence								Other food items[2] (percent)
	I Organism	Percent	II Organism	Percent	III Organism	Percent	IV Organism	Percent	
Little	Chironomid	28	Chaoborus	20	Dragonfly	14	Corixids	10	28
Little Hdqrs.	Dragonfly	63	Molluscs	18	Notonectids	10	Mayfly	3	6
Marl	Dragonfly	68	Notonectids	20	Damselfly	6	Mayfly	4	2
Doyle	Dragonfly	80	Molluscs	8	Mayfly	5	Notonectids	5	2
Slide	Dragonfly	75	Chironomids	19	Mayfly	3	Molluscs	2	1
North Twin	Misc. Diptera	40	Cladocera	35	Mayfly	10	Corixids	7	8
Bass	Fish	33	Molluscs	28	Dragonfly	24	Chironomid	4	11
Norway	Chaoborus	47	Notonectids	23	Leech	10	Molluscs	6	14
South Twin	Higher plants	56	Dragonfly	14	Cladocera	11	Chaoborus	7	12
Ryan	Dragonfly	37	Terr. insect(A)	26	Cladocera	22	Higher plants	3	12

[1] All aquatic insects, except Notonectidae and Corixidae, were represented principally by immature forms. Scientific names are used in the common name sense.

[2] Also includes debris and unidentifiable plant and animal remains.

Predatory animals

On the occasion of each visit to the lakes a close watch was made upon approach to note the presence and activity of any predatory animals. A number of predators were observed on these visits. A pair of loons spent most of the season on Doyle Lake. An otter was observed once at Marl Lake and once at Little Lake. American and hooded mergansers were observed on Slide and Marl lakes. Great blue herons were observed at Bass, Ryan and Marl lakes, and a nest of green herons was found in a tree overhanging Norway Lake. Each lake was visited once every 2 weeks throughout the 1960 season. If more visits had been made, especially in the daily crepuscular periods, I am sure many more predatory animals would have been observed.

About 40 northern pike were gill-netted during the season in Ryan Lake. Several more were found dead following the rotenone treatment. The pike averaged slightly over 17 inches in length. One fingerling trout 10.5 cm in length was found in a pike stomach from Ryan Lake in July. It is probable that these pike entered Ryan Lake from the Denton Creek outlet sometime before mid-April and thus were present in the lake the entire season. A large (length 51 cm) northern pike was killed in the October, 1960 rotenone treatment of South Twin Lake. I doubt if this pike had been in the lake all season.[6]

Water snakes (Natrix sipedon) were seen at Marl, Doyle, Ryan, and Bass lakes. I believe they were present around all of the

---

[6] It was rumored that a local man introduced the pike just before the rotenone treatment to see if it would be recovered in the treatment.

lakes except Little Headquarters. In May, 1959 a water snake caught a legal trout on Marl Lake shortly after the fish were planted.

Snapping turtles were observed in every lake except Little Headquarters. Turtles (several species) caused the destruction of about 320 trout in the gill nets. It was noted in night observations with submerged electric lights that adult snapping turtles frequently swam in the vicinity of concentrations of trout. On two of these occasions in Marl and Slide lakes live trout were captured with a large wound in the dorsal area; these wounds were about one and one-fourth inches long and one-half inch deep. It is doubtful that these fish could have lived for more than a few hours. It is possible that the wounds were bites inflicted by the snapping turtles.

DISCUSSION AND FURTHER EXPERIMENTS

The stocking of trout in waters where they cannot spawn, or maintain a self-sustaining population through recruitment, is a problem of efficiency in making trout of satisfactory size and appearance available to the angler in the greatest quantity. A high rate of depletion in numbers can be expected from the time of planting throughout the existence of the population. Through growth in weight of the individual fish an expansion of the original biomass can be expected, utilizing the food produced in the lake environment. Production is offset by loss from natural mortality. The question of how best to manage for maximum angler harvest entails a determination of the size and numbers of trout to plant, and selection of a lake environment to assure a high rate of growth with a low rate of natural mortality.

In this discussion, attention will be given first to the environmental factors controlling growth of trout, and next, to environmental factors influencing natural mortality. The interaction of growth and mortality will then be discussed with regard to efficiency of the trout population in providing a maximum stock of trout for the angler. Lastly, the relationship of temperature as it affects rainbow trout in the lake environment will be reviewed from the literature and from the experiences of this study.

Environmental factors influencing
growth

The growth in weight of the individual trout varied significantly between the populations in the ten lakes. The magnitude of this difference in growth was large as at the extremes of the range, trout in Little Lake (269 grams) averaged nearly 2.5 times as large as those in Ryan Lake (110 grams) at the end of the 1960 season. The dominant environmental factor that influenced absolute growth was the biomass of the total fish population in each lake. The Spearman Rank Correlation Coefficient between absolute growth and total fish biomass (trout and other species combined) was $r_s = .806^{++}$. This coefficient is positive as the population exhibiting the greatest absolute growth was ranked number one, and the population with the lowest biomass was given first rank as the dependent variable in the non-parametric Spearman test. A linear regression computation was not possible as the total biomass was known only on an ordinal scale. Considering the relatively low power of the Spearman Rank test, however, it is apparent that the relationship between absolute growth and population density would also have been highly significant with the parametric linear regression analysis.

The significant relationship between large absolute growth and low total fish biomass in these lakes is most likely due to the fact that several of the populations were below the hypothetical carrying capacity of the lake and thus growth was influenced by the food supply available to the individual fish. All of the lakes were treated with 0.5 ppm of rotenone in the fall of 1959. Four of the five lakes (Table 23) in which greatest absolute growth occurred contained trout-only fish populations. The fifth (Doyle Lake) contained only a few redbelly dace. Four of the five lakes exhibiting lesser growth of trout contained sizeable populations of non-trout species. These four lakes probably approached carrying capacity much more closely than did the lakes with trout-only populations.

Confronted with the close correlation of absolute growth to total fish biomass it is difficult, if not impossible, to assess other environmental factors influencing trout growth in more than a speculative sense.

The decreased rate of growth in July and August from high temperature does not appear to lessen absolute growth for the season as a whole because it is compensated by very rapid growth in September and October (Fig. 9).

It is possible that the relative size of the littoral zone in each lake was an underlying factor of importance in determining the absolute growth through control of the relative quantity of food produced. The food habits study indicates that benthic organisms provided the bulk of the trout food in nearly all of the lakes. Ball (1948) found that the littoral zone in a southern Michigan lake produced the bulk of the food of the bluegill. In this lake the littoral zone was determined as the area from shore to a depth of

Table 23. Rank of each lake according to the parameters of trout success, 1960

Rank	Final mean weight (grams)	Condition factor K	Natural mortality	Total production (pounds per acre)	Relative efficiency
I	Little 269	Little 1.061	S. Twin .17	Slide 22.96	Little 2.07
II	Hdqrs. 263	Hdqrs. 1.025	Bass .19	Bass 22.93	Bass 2.00
III	Doyle 247	Slide 1.022	Little .25	N. Twin 18.91	Slide 1.71
IV	Marl 239	N. Twin 1.010	Slide .38	Hdqrs. 16.02	Hdqrs. 1.67
V	Slide 230	Doyle 1.000	Norway .40	Doyle 15.58	S. Twin 1.37
VI	N. Twin 211	Marl .992	Hdqrs. .45	S. Twin 12.37	Norway 1.22
VII	Bass 188	Bass .979	Ryan .58	Norway 12.11	Marl 1.14
VIII	Norway 156	Norway .952	N. Twin .65	Little 11.45	N. Twin 1.08
IX	S. Twin 146	S. Twin .934	Marl .69	Marl 10.26	Doyle .86
X	Ryan 110	Ryan .884	Doyle .78	Ryan 5.99	Ryan .76

3 meters--the lower limit of submerged plant growth. Johnson and Hasler (1954) consider the "life zone" that volume of water containing more than 3.0 ppm of dissolved oxygen as the food producing zone for rainbow trout of Wisconsin dystrophic lakes.

The relative size of the littoral zone to a depth of 3 meters, and the oxygenated volume, containing over 5.0 ppm (also more than 0.0 ppm) dissolved oxygen, were portrayed in Figure 21 for each of the ten lakes in this study. I found that the correlation coefficient (r) between absolute growth of trout and large littoral zone as defined by lake bottom area to a depth of 3 meters was r = .803^{++}. This correlation was greater than absolute growth to the lake bottom area of the zone containing over 3.0 ppm of dissolved oxygen (r = .661^{+}) and much greater than to the bottom area of the zone containing more than 0.0 ppm of dissolved oxygen (r = .282^{-}). These relationships, however, are subject to question in light of the correlation between growth and the total biomass of fish as discussed previously. No relationships were apparent by inspection between alkalinity or hydrogen ion content of the water and absolute growth of the trout.

It is possible that the relative size of the littoral zone and the total biomass of the population are both dominant environmental factors in regulating trout growth. Both factors operate to regulate the food supply available to the trout. The size of the littoral zone is of importance in determining the total supply of food. The density of the population determines the rate of cropping of this food. The size of the littoral zone was fixed in the individual lakes, but the density of the population could fluctuate over a wide range. Thus the food supply produced varied between the lakes, but population density was the immediate factor that determined how much food was available to the individual trout.

Turning to discussion of trout growth in the individual lakes several observations can be made which shed additional light on the relationship of trout growth to the available food supply. In Bass Lake the growth of the rainbow trout (Table 8) was rapid until about the time of the June bluegill hatch after which the rate of growth in weight declined rapidly until it was negative in value. Bass Lake has a small littoral zone. Only 28 percent of the bottom is included in the 0 to 3 meter range of depth. It seems apparent that the trout population had an ample food supply until the bluegill hatch occurred. The combined-species fish population probably expanded rapidly thereafter, depleting the food supply to the point that the trout could not meet maintenance requirements.

Ryan and South Twin lakes show a slow growth rate of the trout all season. It is believed that each of these lakes had a relatively high population of non-trout species all season and that the food supply was insufficient to allow the trout to make rapid growth. It is also possible that the metabolic scope for activity of the trout was lower than that of the competing species making the trout a relatively poor competitor for the available food when other fish species were present.

trac

sm

and

Th

co

en

wa

in

av

to

r

a

i

The reasoning expressed above seems to be completely contradicted by the trout population in North Twin Lake. This lake has a small littoral zone, and contained a relatively large biomass of trout and non-trout species. Yet trout growth was fairly rapid (Table 23). The explanation may lie in the fact that North Twin Lake is atypical compared to the other lakes. This lake received a heavy organic enrichment from slaughterhouse wastes. The population of Cladocera was high throughout the season, and undoubtedly the production of invertebrate bottom organisms was very high in the small area available to them. Apparently the food supply was sufficiently high to allow rapid growth of the entire population.

Norway Lake, on the other hand, had a relatively low growth rate although no fish other than trout were present. Norway Lake has a precipitous basin slope starting almost at the shoreline. The water is soft and very turbid throughout the season. Consequently, the available food supply of benthic organisms is believed to have been very low. The food habit analyses (Tables 21 and 22) corroborate this view as littoral benthic organisms made up only a small portion of the trout food. It would seem that the mean standing crop of 16.9 pounds per acre was nearly equal to the carrying capacity of this relatively unproductive lake.

In the remaining lakes trout growth was fairly rapid and did not differ markedly between lakes. All of these lakes contained trout-only populations. There was a slight indication that growth was reduced as biomass of trout increased.

1961 experiments on competition affecting trout growth

The finding, from the 1960 studies, that relative size of the standing crop of fish was the dominant environmental factor affecting absolute growth of trout prompted a decision to use the 1961 year of field investigation for further experimentation in this area. Five lakes from the 1960 studies, namely; Doyle, Little Headquarters, Slide, Little, and Ryan, were selected for the 1961 investigations. Each of these lakes had been treated with rotenone in October, 1960 to eliminate the fish population. They were stocked on April 20, 1961, at various rates to establish markedly different biomasses of fish in each lake (Table 24). The objective and results of each lake experiment are summarized in the following paragraphs.

Doyle Lake.--This lake was selected as the control, and planted at nearly the same rate with rainbow trout in both 1960 (20 pounds per acre) and 1961 (23 pounds per acre). The slight difference in planting rate resulted from the fingerling trout being of larger size in 1961.[7] The growth rate of trout was nearly identical in both years (Fig. 23).

---

[7]The fingerlings planted in 1961 had a mean weight of 12 grams as compared to a mean weight of 1.1 grams for the 1960 plant. These fish were the smallest fingerlings available from the hatcheries in 1961 and thus were planted in Little, Marl, and Little Headquarters lakes, as well as Doyle, in these experiments.

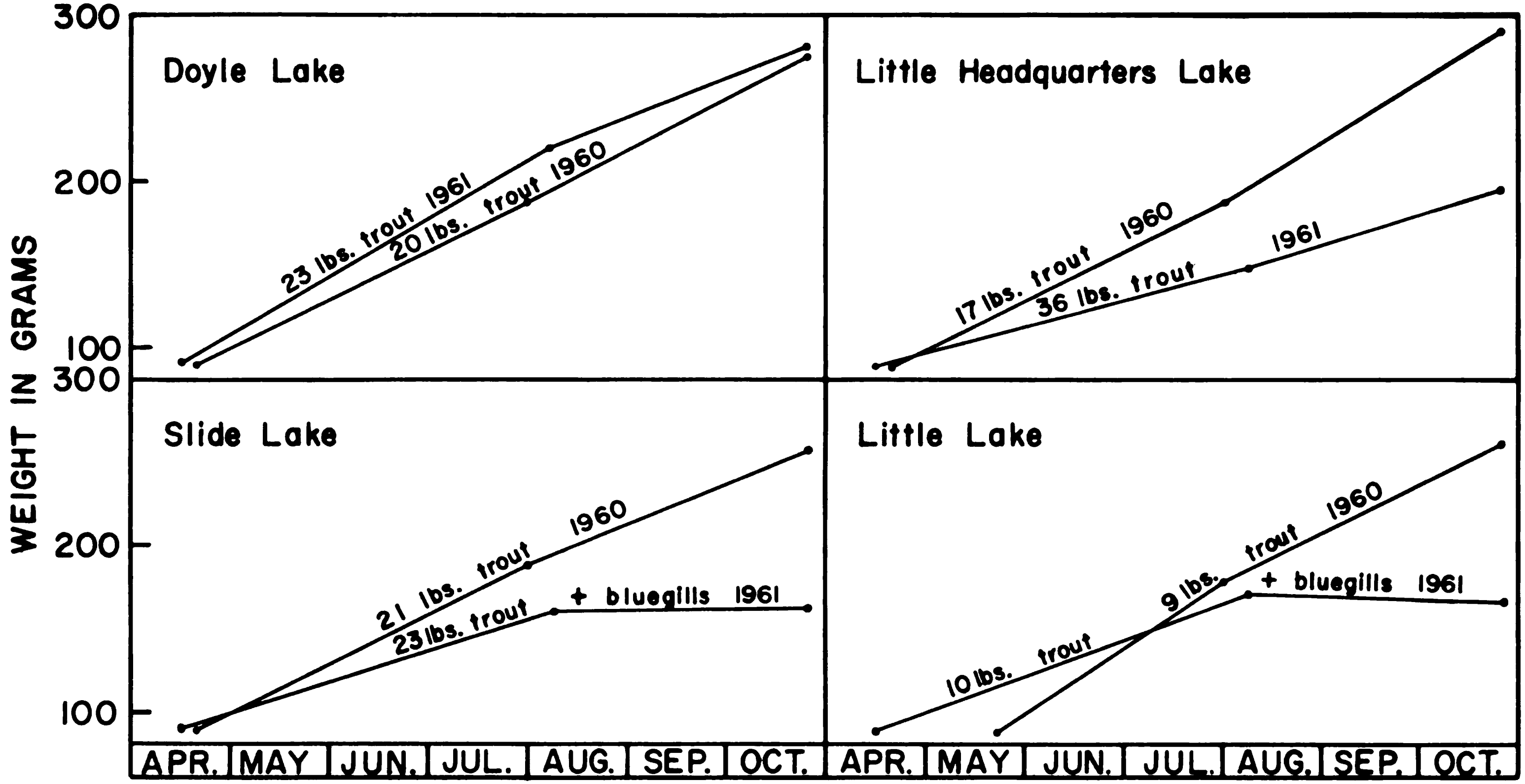


Fig. 23. Comparison of rainbow trout growth in weight in relation to the rate of stocking (pounds per acre) and to competition from young-of-year bluegills.

Little Headquarters.--The rate of planting of both legal and fingerling trout was approximately doubled in 1961 (36 pounds per acre) over the 1960 rate (17 pounds per acre). The increased biomass in 1961 caused a significant reduction in final size. The final mean weight in 1961 was 198 grams as compared to 291 grams for the NC[8] group in 1960. The condition factor (K) showed a corresponding decrease from 1.071 (1960) to .971 (1961).

Slide Lake.--The rate of planting of trout was approximately the same in 1961 (23 pounds per acre) as in 1960 (21 pounds per acre). These planting rates correspond with those in Doyle Lake. In Slide Lake, in 1961, approximately 50 adult bluegills were released just after the trout were planted. These bluegills comprised less than 5 percent of the trout biomass. The objective was to determine the effect of their young-of-the-year progeny on trout growth, not of the adults alone. A good hatch of young bluegills occurred in June and they were observed in abundance thereafter until the final trout collection in October. The final mean weight of the legal trout in 1961 was 164 grams, as compared to 260 grams for the NC group in 1960. The 1961 K factor was .895 compared to 1.042 for the NC group in 1960.

Little Lake.--This lake was planted at approximately one-half of the rate in Doyle Lake with legal trout in both 1960 (9 pounds

---

[8] Comparison of absolute growth of the 1961 legal trout is made with the 1960 NC group in Doyle, Little Headquarters, and Slide lakes, because these groups were both planted in April and are more directly comparable. In Little Lake the comparison of trout growth in 1961 must be with the 1960 A and LP groups as no NC fish were available.

pe

ac

pr

le

th

lo

c

t

b

r

v

2

i

t

s

g

tr

per acre) and 1961 (10 pounds per acre). In addition approximately 50 adult bluegills were introduced with a hatch of young-of-the-year progeny the same as in Slide Lake. The final mean weight of the legal trout in 1961 was 169 grams, as compared with 269 grams for the A and LP groups in 1960. The K factor of .889 in 1961 was much lower than the K factor of 1.087 in 1960.

Ryan Lake.--Only 200 legal trout were planted in 1961 as compared with 1,480 legal and 1,440 fingerling trout in 1960. Further, the barrier screen remained intact throughout the season and the biomass of non-trout species was much lower than in 1960. With the reduced biomass the trout grew rapidly in 1961. Twelve trout caught with gill nets on August 17, 1961, averaged 30.1 cm in length, and 295 grams in weight. Anglers reported catching trout from 13 to 15 inches in length in late August. On October 26 only 2 trout were taken in the gill nets (28.5 cm in mean length, 216 grams mean weight). All of these trout were larger than the final size of the trout in 1960 (average weight NC group, 112 grams), indicating that the poor trout growth in Ryan Lake in 1960 was due to the large biomass of fish present, not to other physical or chemical characteristics of the lake.

The results of these experiments (except Ryan Lake) are summarized in Table 25. In Figure 23 the results are portrayed graphically. In 1960 at planting rates of 9 to 21 pounds per acre the trout in all four lakes grew at similar rates. In Doyle Lake in 1961

Table 24. Summary of trout stocking statistics for experiments on effect of trout population density and young-of-year bluegill competition[1] on trout growth

Lake and experiment number	Year	Size class	Number per acre	Pounds per acre	Mean length (cm)	Mean weight (grams)
1. Medium trout (1960) vs medium trout (1961) (control)						
Doyle	1960	Legal	101	20.0	21	90
	1960	Fing.	100	0.2	5	1
	1961	Legal	100	19.8	20	90
	1961	Fing.	100	2.6	10	12
2. Medium trout (1960) vs heavy trout (1961)						
Little Headquarters	1960	Legal	88	17.2	21	90
	1960	Fing.	80	0.2	5	1
	1961	Legal	80	31.7	20	90
	1961	Fing.	161	4.3	10	12
3. Medium trout (1960) vs medium trout + bluegills (1961)						
Slide	1960	Legal	106	20.8	21	90
	1960	Fing.	102	0.2	5	1
	1961	Legal	102	20.2	20	90
	1961	Fing.	102	2.7	10	12
4. Light trout (1960) vs light trout + bluegills (1961)						
Little	1960	Legal	42	8.5	21	91
	1960	Fing.	84	0.2	5	1
	1961	Legal	42	8.3	20	90
	1961	Fing.	84	2.2	10	12

[1]Approximately 50 adult bluegill spawners released in Slide and in Little lakes in 1961.

Table 25. Comparison of length, weight, and condition factor of trout in experiments on the effects of trout population density and of young-of-year bluegill competition on trout growth

Lake and experiment number	Trout group	Initial		Midsummer[1]			Final[2]			Difference (final)	
		Length (cm)	Weight (grams)	Length (cm)	Weight (grams)	K	Length (cm)	Weight (grams)	K	Weight (grams)	K
1. Medium trout (1960) vs medium trout (1961)											
Doyle	1960 Legal	21	90	27	188	1.001	30	279	1.004	--	--
	1961 Legal	20	90	28	222	1.020	30	283	1.006	+4	+.002
2. Medium trout (1960) vs heavy trout (1961)											
Little	1960 Legal	21	90	26	189	1.056	30	291	1.071	--	--
Headquarters	1961 Legal	20	90	25	148	.913	27	198	.971	-93	-.100
3. Medium trout (1960) vs medium trout + bluegills (1961)											
Slide	1960 Legal	21	90	27	189	.993	29	260	1.042	--	--
	1961 Legal	20	90	26	161	.918	26	164	.895	-96	-.147
4. Light trout (1960) vs light trout + bluegills (1961)											
Little	1960 Legal[3]	21	91	26	180	1.035	29	265	1.087	--	--
	1961 Legal	20	90	27	176	.912	27	169	.889	-96	-.198

[1] 1960 group collected on July 30; 1961 group collected on August 8.

[2] Both 1960 and 1961 groups collected October 25.

[3] Planted May 24 (all other initial groups planted April 14 to 20).

(planting rates of 23 pounds per acre) the trout grew at a similar rate to 1960, but in Little Headquarters Lake with the planting rate doubled growth decreased by nearly 50 percent (from 201 grams in 1960 to 108 grams in 1961). Apparently this heavier rate of stocking caused the biomass of trout present to pass some critical point of the food supply whereafter growth dropped sharply. It will be noted from Figure 23, that the absolute growth rate remained relatively constant throughout the year in Little Headquarters Lake with a trout-only population. In Slide Lake and Little Lake (1961) the young-of-year bluegill population reduced trout growth approximately 50 pereent from 1960 similar to the effect of the double rate of trout planting in Little Headquarters Lake. The growth curves in Figure 23 show that the trout in Little and Slide lakes made practically no growth in weight after mid-August. This is the same phenomenon observed in Bass Lake in 1960 (Fig. 9) when trout growth ceased by mid-August following a bluegill hatch. The light rate of trout planting (10 pounds per acre) in Little Lake had no practical effect in sustaining trout growth, over the medium (23 pounds per acre) rate of trout stocking in Slide Lake, after the bluegill hatch occurred.

It is apparent that the rainbow trout can grow rapidly in any of these lakes at low population levels (less than 20 pounds per acre). However, either increasing the biomass of trout materially, or adding competing species of fish to the population, will suppress the rate of growth. The first-year progeny of a competing species such as the bluegill demonstrates in these studies how severe inter-specific competition can be in limiting growth of the trout, as in nearly every instance trout growth declined to practically zero within a few weeks after a bluegill hatch. There is certainly a reduction in the food supply available for the individual trout with any material increase in total fish biomass. It is possible that some sort of "crowding factor" operates to limit trout growth beyond simple food supply in the mixed species population. There is evidence that temperature controls metabolism of these various species in water above 65 F and renders the trout the poorer competitor (cf. discussion on temperature).

The lakes in the 1961 experiment had been poisoned with rotenone in both the spring and fall of 1959 and in the fall of 1960 to eliminate the existing fish populations. In Figure 24 the mean growth in weight of each successive trout population in Doyle Lake is portrayed. Although the actual mean standing crop of trout present was not ascertained in 1959 and 1961, it is believed that the standing crop was materially larger in each of the successive annual trout populations. There is no evidence that the repeated rotenone treatments adversely affected trout growth, rather, there is some indication that the growth rate was more rapid in 1960 and 1961 than in 1959.

Mortality

Fishing mortality has been discussed earlier in this paper so only natural mortality will be discussed here. The rate of natural mortality was closely estimated in each lake, but little is known of the

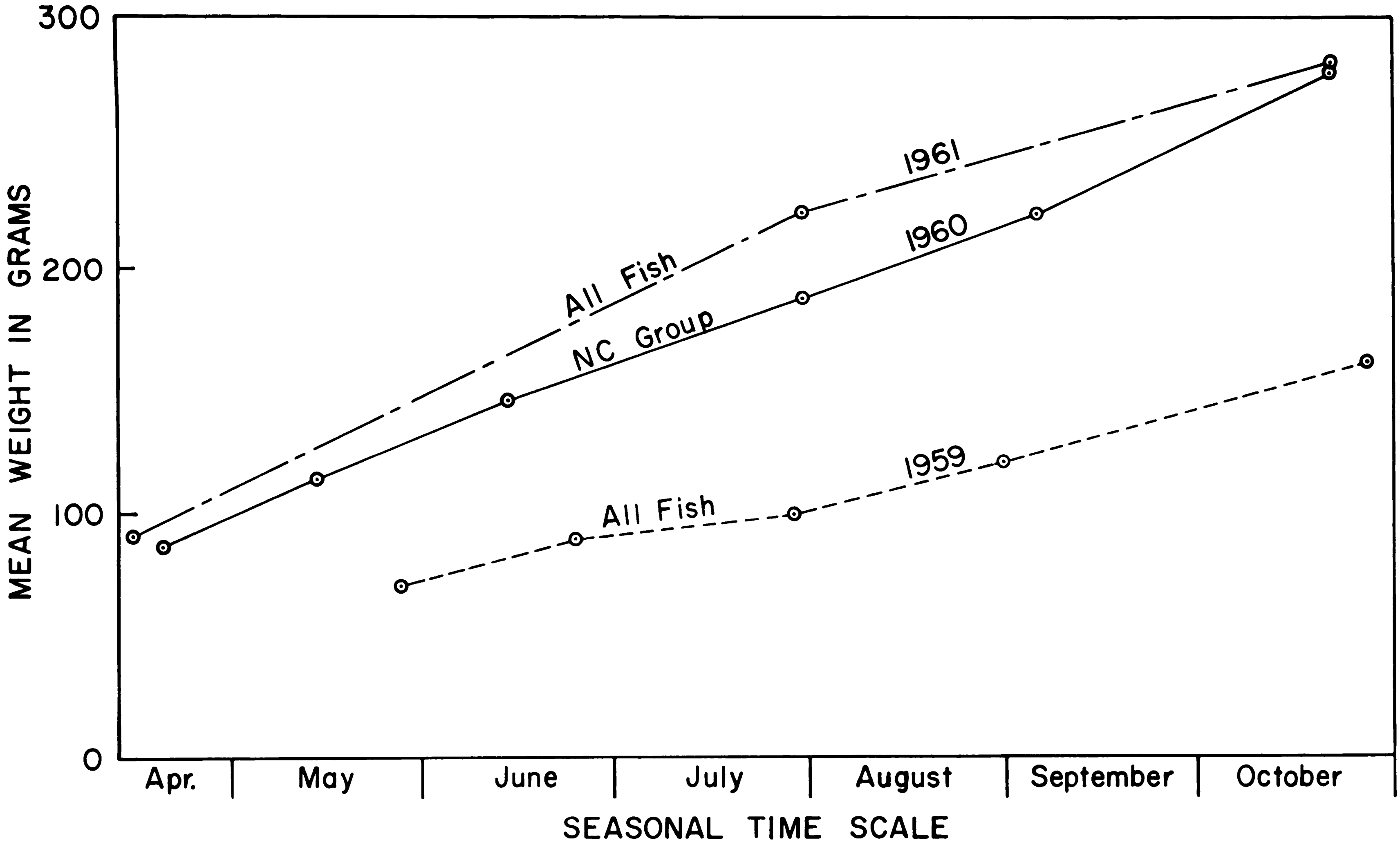


Fig. 24. Comparison of absolute growth of trout in Doyle Lake 1959, 1960, 1961. The mean standing crop of trout was the lowest in 1959, higher in 1960, and highest in 1961.

actual causes of death. The most likely source of extensive natural mortality is the loss of trout to predatory animals.

Natural mortality, as the ratio of loss from natural deaths to the population excluding fish removed by the fishery, is summarized for the ten lakes as a parameter of trout success in Table 23. This ratio of natural mortality ranged from a low of .17 in South Twin Lake to a high of .78 in Doyle Lake.

There is considerable circumstantial evidence that predation was closely associated with high natural mortality in Ryan, Marl and Doyle lakes. Ryan Lake had a loss of 661 trout attributable to natural mortality. Forty northern pike were taken from this lake with gill nets during the 1960 season, and several more were found dead following the rotenone treatment. A few of these pike were dissected for stomach content analysis. One stomach contained a rainbow trout fingerling (length, 10.5 cm). Doyle Lake sustained a loss of 1,352 trout attributable to natural mortality. This lake supported a pair of loons for nearly the entire season (no young loons were observed). The loon is a notable predator of fish (Olsen and Marshall, 1952). As trout were the only fish present in Doyle Lake except for redbelly dace, it seems evident that many of them fell prey to the loons. In Marl and Slide lakes an estimated 331 and 256 trout were lost respectively to natural mortality. These were the only lakes where American mergansers were observed, although it is noteworthy that each of these lakes contained a large population of snapping turtles.

These four lakes had a combined natural mortality of about 2,600 trout or 84 percent of 3,100 trout estimated lost from natural causes of death in the ten lakes. The trout planted in these four lakes comprised 64.8 percent of the total plant for comparison.

Three of the lakes; Little Headquarters, South Twin, and Bass, have permanent residences and considerable human activity throughout the season. As losses from natural mortality were relatively low in these lakes,it is possible that predators were frightened away to some extent by human activity. Human occupancy might be an advantage in trout management on small lakes.

The evidence is mostly negative with regard to trout loss from other natural causes. It was found that initial mortality after planting was very low. Thus the loss from handling injury, temperature shock, osmotic shock, or any other mortality attributable to handling and transfer to new waters was negligible, although such losses have often been substantial in fish handled for laboratory purposes (Black, 1957).

It is unlikely that escapement from the lakes could have occurred as all of the lakes were either landlocked or had effective screens after the trout were planted.

Throughout the experiments no trout were taken that showed recognizable symptoms of disease. None of the trout examined showed heavy infestation of either external or internal parasites. Hence these two factors as a possible source of natural mortality are also considered negligible.

The coefficient of correlation (r) between natural mortality and absolute growth was only .126. Thus it seems likely that the environmental factors responsible for natural mortality are quite independent of those factors that limit growth. Starvation would thus appear insignificant as a cause of death. In fact there is little indication that any "stress" arising from high natural mortality affected trout growth, or vice versa.

Production

Production of trout was discussed at some length in conjunction with population dynamics. In that discussion it was pointed out that production, in the sense of total growth of all fish whether or not they live until the end of the season, is a function of the instantaneous rate of growth and the instantaneous rate of mortality. Production in the quantitative sense is also dependent on the total number of trout in the population inasmuch as stock size forms the base upon which production is realized. Thus the total weight of trout produced is dependent upon the rate of stocking as well as upon the rates of growth and mortality.

In New York ponds Eipper (1959) found that production increased with an increase in the rate of stocking up to 2,400 fingerling trout per acre despite steady diminution in the rate of growth. There is a compensating effect of greater growth to maintain production at lower population densities but it is not effective in a practical sense at low rates of planting. For example, 42 legal trout were planted per acre in Little Lake in 1960 in comparison with a plant of 106 legal trout per acre in Slide Lake. The rate of growth was higher and the rate of mortality lower in Little Lake (Table 23) than the corresponding rates in Slide Lake, but Slide Lake produced 22.96 pounds of trout per acre as compared to 11.45 pounds per acre produced in Little Lake. In this case the rate of stocking in Little Lake was too low for efficient production, or a favorable economic return based upon the productive capacity of the lakes and costs of the rotenone treatment. As these lakes were not heavily fished it would seem that the best planting rates should have been still higher if an intensive fishery had been expected.

The efficiency index $\frac{(Y + Wt)}{W_o}$ provides a test of the efficiency of a stocked trout population in making fish available to the angler. Of the ten lakes in this study only in Little Headquarters Lake were more fish (19.2 pounds per acre) taken in the fishery than were originally stocked (17.2 pounds per acre). The final standing crop in October was 9.5 pounds per acre to give an efficiency index of 1.67 for Little Headquarters Lake at that time (1.67 times as many fish by weight had been caught or remained to be caught as had originally been stocked). By comparison eight of the lakes had an efficiency index of 1.00 or over for the season, and of these Bass and Little lakes had high values of 2.00 and 2.07 respectively (Table 23). In the other two lakes, Doyle and Ryan, the efficiency index ratings were 0.86 and 0.76 respectively. These values below 1.00 give a good indication that the original weight of trout planted would not have been harvested by anglers. On this basis, the populations in Doyle and Ryan lakes could be classified as failures in the management sense.

It was found that the efficiency index in these ten lakes was more dependent upon natural mortality ($r = .707^{++}$) than on absolute growth in weight ($r = .424^{-}$). This point can have considerable management significance, especially in lakes where high natural mortality is expected from such predators as loons and mergansers. For example, in Doyle Lake the trout made relatively good growth, but natural mortality was high (probably loon predation) and the efficiency index was consequently low (.86 in October). On the other hand, in plants of legal trout in streams, on a put-and-take basis where no growth is expected, the efficiency index will be low (1.00 or below).

Temperature as an environmental factor

Trout are fishes of the colder waters in the United States. In management it is often necessary to consider in detail many of the warmer marginal waters relative to suitability for trout. In addition to the demands for trout fishing waters in general, many small lakes and ponds in the northern latitudes are difficult to manage for balanced prey-predator populations of other fishes, but are capable of producing trout satisfactorily as a single species. Also the relatively fast growth of trout makes them valuable as an interim population in waters chemically rehabilitated for combination-game fish populations, i.e., to provide fishing during the time required to rebuild a "balanced" population of other fishes. These demands for trout management in relatively warm-water environments necessitate an accurate appraisal of the thermal requirements of trout.

Fish, being aquatic poikilotherms, lack a means of maintaining a body temperature independent from the external environment. The body tissues are constantly being brought into equilibrium with the external temperature at the gill surface by the circulatory system. Only slight differences in the internal and external temperatures, due to metabolism and time lag of change, may exist. Thus, the fundamental thermal requirement of these fishes is an external environmental temperature suitable to the internal tissues throughout life (Brett, 1956).

The upper and lower limits of temperature which trout can withstand define the extremes of the tolerable thermal environment. This is defined as the zone of tolerance. The lethal temperature is theoretically conceived as that temperature which 50 percent of a population could withstand for infinite time. Experimentally it is determined by subjecting sub-samples of fish to a series of temperatures, the highest of which result in complete mortality of the sample. The period of tolerance prior to death of each sub-sample is called the resistance time (Fry, 1947). Although somewhat oversimplified it can be stated that such experiments demonstrate that starting at low temperatures, the median resistance time of each sub-sample is relatively unlimited.

Upon reaching some definite higher point in the temperature series, the resistance times become limited and progressively shorter as the sub-samples are subjected to increasingly higher temperatures. This inflection in resistance times marks the transition from the tolerance zone of temperature to the lethal zone and is called the upper *incipient lethal level of temperature* (UILT). By means of the incipient lethal levels, tolerance zones of the trout can be quite definitely ascertained.

The Salmonidae have the lowest thermal tolerance found to date, with maximum upper lethal levels barely exceeding 25 C (77 F), according to Brett (1956). Available figures for estimated UILT for the three species of trout are: brook trout 24.2 C (75.6 F), Brett, 1952; rainbow trout 25.7 C (78.3 F), Black, 1953; and brown trout 25.5 C (77.9 F), Brett, 1952. These temperatures should not be considered absolute. For example, the rainbow trout value is for kamloops trout in British Columbia, acclimated at a temperature of 11 C. A slightly higher UILT could be expected for different genetic races or possibly upon complete acclimatization to higher temperature.

The brook trout has a greater cold-tolerance than any species yet reported (Brett, 1956). Evidence that the rainbow and brown trout are less tolerant to cold than other genera of Salmonidae is indicated by their comparative distribution. The trout of the genus *Salmo* are definitely more southerly in range across the North American continent (Rounsefell, 1958), than the genus *Salvelinus*.

The upper and lower limits provided by the zone of tolerance over a complete range of thermal acclimation defines the boundary between life and death. Within these limits, temperature cannot be a primary cause of mortality. It must be recognized that these limits do not reveal what can be tolerated for shorter intervals outside the zone of tolerance or the implications of the role of temperature on other physiological or ecological functions of the trout (Brett, 1959).

Fishes have varying degrees of ability to extend their temperature tolerance through acclimation. It appears that the rate of increase in ability to tolerate higher temperatures is relatively rapid. Conversely, the loss in this increased tolerance, and the gain in resistance to low temperatures, are inherently slower processes. These rates appear to be governed by the rate of metabolism, which, if depressed by a low environmental temperature, automatically reduces the rate of acclimation (Brett, 1956). The brook trout can increase its heat tolerance about 5 C over the range of acclimation temperatures which is probably somewhat lower than that of the rainbow and brown trout (Brett, 1956).

Outside the limits of the zone of tolerance it is of importance that the resistance time to death is in the magnitude of several hours at temperatures just above the incipient lethal level. The resistance time to death then declines progressively over a range of 5 to 10 C before approaching zero. The result of the resistance time to death is that it enables the trout to live for finite periods of time in waters of such temperature that would eventually be lethal. The resistance time thus enables the trout to make forays for limited periods of time in waters above the UILT, to survive diurnal fluctuations of water temperature above the UILT, and to escape other peaks of environmental temperature ordinarily considered lethal. The resistance time to death accounts for much of the confusion that exists in field observations of trout relative to supposedly lethal temperatures.

In the 1960 experiments on the ten lakes of this study, there was no evidence that any trout mortality occurred as a result of high temperatures. In the hot weather of late August and early September water temperatures in the deep area of Little Headquarters Lake reached 74 F (Fig. 34, Appendix). This temperature was about 4 F lower than the upper UILT of 78 F of the rainbow trout. However, a mortality that is worthy of description in this discussion and that can be attributed to heat death did occur during extremely warm weather of 1959 on Little Headquarters Lake. On August 28, 1959, at 11:30 AM (air temperature 85 F) 31 dead legal, and 3 dead fingerling rainbow trout were picked up around Little Headquarters Lake (5.5 acres). Two fingerlings were observed in distress and were easily captured from the water surface by hand. The water temperature at this time ranged from 80.0 F at the surface to 78.8 F at a depth of 9 feet (the deepest point near the center of the lake). A small spring with a temperature of 60 F and an estimated flow of approximately 5 gallons per minute fed into a shallow area at the southeast corner of the lake. About 20 legal trout were observed crowded into this small spring area. On September 1, 1959, the lake was rechecked to follow the progress of the trout mortality. On this date the air temperature at 10:45 AM was 70 F. Water temperatures ranged from 75.9 F at the surface to 74.5 F at the bottom. Thirteen additional legal-size trout were found around the lake all of which were in an advanced state of decomposition. No freshly dead trout were found and it was concluded that the losses from heat death had ceased. Subsequent fishing reports and gill net catches indicated that the total loss in this observed mortality could have been no more than a small fraction of the population. This field observation substantiates the physiological laboratory findings on the UILT of rainbow trout, and demonstrates the ecological significance of resistance time to death in relation to trout survival in a natural environment.

As important as consideration of lethal temperature may be, the effect of temperature as a controlling factor on trout activity is equally important, and much more subtle and complex throughout the range of thermal tolerance. Fortunately much attention has been given to this area of research in recent years. Fry (1947) demonstrated that the performance or scope for activity was related to the difference between resting metabolism and active metabolism. Thus a means of examining the influence of temperature as a controlling factor was provided. Temperature as a controlling factor of metabolism is operative at all levels; hence, the trout never escapes the influence imposed throughout the range of thermal tolerance.

The scope for activity over the tolerable thermal range varies with each species of fish. The scope for activity of the brook trout increases from 0 C upward, reaching a peak at about 19 C (66.2 F) from which point it decreases to the upper lethal temperature (Fry, 1947). The rainbow and brown trout by contrast appear capable of increasing the scope for activity up to nearly the UILT (Brett, 1956). Thus the scope-for-activity concept may provide further insight into the ability of the various Salmonidae to compete with each other and with other groups of fishes for food and space. Brook trout, for example, are not usually found in abundance in natural environments exceeding 19 C (Creaser, 1930). It is possible that brook trout are unable to compete successfully with other species of fish as its scope for activity declines at temperatures higher than 19 C. The scope for activity of competing species is greater above 19 C than that of the brook trout, giving these species the thermal advantage in competition for food and space.

The evidence of the current study indicates that rainbow trout were poor competitors with other fish species found in the lakes. Wherever non-trout species occurred, the growth of trout was suppressed. In Bass Lake, for example, the rainbow trout growth in weight ceased after an early summer hatch of bluegills. The trout actually lost sufficient weight to cause production to be a negative value the remainder of the season. The bluegills during this period exhibited rapid growth and high K factor. The available food in this deep, clear lake was restricted principally to the relatively warm littoral zone, thus a greater scope of activity for the bluegills than for the trout would appear to be a plausible explanation for this phenomenon. Similar effects on reduced trout growth and K factors were described in the 1961 experiments on Slide and Little lakes where young-of-the-year bluegills were competing. The cessation of growth and decline in K was evident as soon as the young-of-the-year bluegills appeared. In 1960 pure trout populations in these same lakes exhibited rapid growth in weight and relatively high condition (K) factors throughout the year.

Two other aspects of temperature are of importance in assessing the response of trout to varied thermal conditions. These are the _preferred temperature_ of the species and temperature as a _directive factor_.

Trout, like other fishes, often congregate within a segment of the thermal range available to them. In laboratory experiments the segment (or point) of the thermal range that trout select is termed the _preferred temperature_. In repeated experiments over a range of acclimation temperatures, the point at which the preferred temperature equals the acclimation temperature is defined as the _final preferendum_ (Fry, 1947).

The available data on final preferenda for the brook, brown, and rainbow trout were summarized by Ferguson (1958) as follows:

Salvelinus fontinalis	14.0-16.0 C	Graham, 1949; Fisher and Elson, 1950

Salmo trutta	12.4-17.6 C	Tait, 1958
Salmo gairdneri	13.6 C	Garside and Tait, 1958a

In a later publication, Garside and Tait (1958b) give the final preferendum of the rainbow trout as 13.0 C. It is interesting to note in Garside and Tait's experiments that the preferred temperature of the rainbow trout was 3 C to 5 C lower when they were acclimated to 20 C than when they were acclimated to 5 C. The authors point out that these results are statistically significant although no other species have been found that exhibit the same phenomenon. No attempt to explain this phenomenon was made.

Various attempts have been made to relate the final preferendum of fishes, as determined in the laboratory, to the maximum scope for activity and to behavior in the natural environment. Fry and Hart (1948) in studying goldfish, found that the final preferendum and the optimum temperature for cruising speed corresponded closely. Fisher and Elson (1950) measured the length of initial dart in response to electric stimulus for brook trout and Atlantic salmon (_Salmo salar_) parr at various temperatures. The maximum response occurred in the region of the preferred temperature. These examples would indicate that the final preferendum and the scope for maximum activity are closely related.

Through experiments using the method of conditioned response, many fishes have been found to be extremely sensitive to detecting slight changes (less than 0.05 C) in temperature (Brown, 1957). The survival value to trout of response to temperature change to escape lethal temperature, or to move to areas for greater scope of activity is apparent. The response of fish to such temperature change can be regarded as the directive factor of temperature. Many workers regard temperature as a directive factor in the spawning and migration of trout (Brett, 1956).

The observation cited from Little Headquarters Lake with reference to heat mortality described the crowding of trout into a cool spring area to escape the generally lethal temperature condition existing at the time. This field observation illustrates clearly trout response to temperature as a directive factor. It can be assumed that trout would seek out any cool areas in the natural environment to escape lethal temperature conditions if such cool water were available. Many cool spring-water areas exist in otherwise warm streams and lakes. These refuge areas would tend to minimize actual mortality from heat death in waters which otherwise would be submarginal for trout.

I fail to see a clear distinction between the preferred temperature of fish and temperature as a directive factor. It would seem that response of the fish to seek out areas of preferred temperature is merely an example of temperature operating as a directive factor.

In summary, the role of temperature determining the survival and well-being of trout is a multiple one. Outside the limits of the zone of tolerance temperature acts as a lethal factor if not relieved within the resistance time of the trout. Temperature constantly conditions the trout to the environment through acclimation, while governing the scope for activity through control of metabolism. Sensitivity of trout to small gradients of temperature results in temperature acting as a directive factor of benefit in essential activities and survival, and enables the trout to select areas of favorable preferred temperature.

Temperature of the aquatic environment is a major factor determining its suitability for trout management. Temperature acts through control of metabolism to limit the maximum scope for activity of trout to relatively cool water in comparison with most other associated fish species. As water temperature of the environment becomes progressively warmer beyond some optimum level for trout activity (possibly the final preferendum), the competitive ability of the trout declines concurrent with an increase in the competitive ability of most other associated species. These changes in competitive ability progressively limit the success of the trout in favor of the competing species over a thermal range of 10 to 20 F before the upper incipient lethal temperature of the trout is reached. The relatively high (78 F) UILT of rainbow trout; the safeguard inherent in resistance time to death at temperatures above the UILT; and the response to temperature gradient as a directive factor to escape heat mortality, lead me to conclude that heat death of trout from lethal temperature conditions is of secondary importance in limiting trout populations to the factor of competition.

Historically more attention has been given to lethal temperature than inter-specific competition in the determination of maximum temperature limits for trout habitat. Embody (1921) set a criterion of 74 F as the maximum limit of waters suitable for trout management. In a later paper (1927) he stated that the maximum tolerance level for trout was 75 F. In the succeeding decade Hubbs and Eschmeyer (1938) lowered the maximum temperature limit to 70 F as a criterion for brook, brown, and rainbow trout. Cooper (1939) in proposing management recommendations for lakes in Maine defined "trout water" as water with an upper temperature limit of 70 F with a minimum dissolved oxygen content of 5.0 ppm. Cooper discussed the effects of warm-water fish species competition with trout, but did not attempt to relate it to temperature of the water. In the 1940's practicing field biologists tended to be more conservative than preceding observers on temperature criteria for trout. In Michigan the tendency was to select only ground-water spring ponds and oligotrophic lakes for trout management (Lagler, 1956).

In recent years the widespread use of rotenone and other fish toxicants to control competing species in warm-water lakes has done much to lessen the conservatism toward cold-water specification in the selection of lakes for trout management (Johnson and Hasler, 1954). Eipper (1960) specifies a maximum temperature of 74 F at the bottom of New York farm ponds as the highest temperature suitable for trout management.

The temperature requirements for suitable trout habitat can be stated in this way. As the upper incipient lethal temperature of rainbow trout is 78 F, suitable lakes for rainbow trout management should contain some water not exceeding this temperature at all times that is otherwise capable of sustaining trout. In some small lakes and ponds where trout are preferred over other species, trout management can be successful even if a loss of trout is experienced occasionally over a period of years. In these warm-water habitats control of competing species is necessary as trout cannot compete successfully with most other species of fish. If temperature is to control competition to favor trout the lake or pond temperature should remain below 65 F throughout the year. This condition can be met in deep, stratified (oligotrophic) lakes where a cold, well oxygenated stratum of water is found throughout the year, or in cold lakes such as those at high altitude or latitude where annual temperatures rarely exceed 65 F.

REFERENCES CITED

American Public Health Association, Inc. 1960. Standard methods for the examination of water and waste water. 11th Ed. Am. Pub. Health Assoc., Inc., New York, 626 p.

Anderson, Richard O. 1959. The influence of season and temperature on growth of the bluegill, Lepomis macrochirus Rafinesque. Ph.D. thesis. Univ. of Michigan. 133 p.

Ball, Robert C. 1948. Relationship between available fish food, feeding habits of fish and total fish production in a Michigan lake. Tech. Bull. 206, Mich. State Univ., Agr. Exp. Sta., 59 p.

Black, E. C. 1953. Upper lethal temperatures of some British Columbia fresh-water fishes. J. Fish. Res. Bd. Canada, 10: 196-210.

Black, V. S. 1957. Excretion and osmo regulation, p. 163-205. In M. E. Brown [ed.] The physiology of fishes. Vol. 1--Metabolism. Academic Press, Inc., New York.

Brett, J. R. 1946. Rate of gain of heat-tolerance in goldfish (Carassius auratus). Publ. Ontario Fish. Res. Lab., 64: 9-28.

__________. 1952. Temperature tolerance in young Pacific salmon, genus Oncorhynchus. J. Fish. Res. Bd. Canada, 9: 265-323.

__________. 1956. Some principles in the thermal requirements of fishes. Quart. Rev. Biol., 31(2): 75-87.

__________. 1959. Thermal requirements of fish--three decades of study, 1940-1970. Trans. Sec. Sem. Biol. Prob. Water Poll., U. S. Public Health Service.

Brown, Margaret E. 1946. The growth of brown trout (Salmo trutta, Linn.). I. Factors influencing the growth of trout fry. J. Exp. Biol., 22(344): 118-129.

__________. 1957. Experimental studies on growth, p. 361-400. In M. E. Brown [ed.] The physiology of fishes. Vol. 1--Metabolism. Academic Press, Inc. New York

Burdick, Milton E., and E. L. Cooper. 1956. Growth rate, survival, and harvest of fingerling rainbow trout planted in Weber Lake, Wisconsin. J. Wildl. Mgmt., 20(3): 233-239.

Clarke, G. L., W. T. Edmondson, and W. E. Ricker. 1946. Mathematical formulation of biological productivity. Ecol. Monographs, 16: 336-337.

Cooper, Edwin L. 1953. Periodicity of growth and change of condition of brook trout (Salvelinus fontinalis) in three Michigan trout streams. Copeia 1953 (2): 107-114.

__________. 1959. Trout stocking as an aid to fish management. Bull. 663, Penn. State Univ., Agr. Exp. Sta., 21 p.

Cooper, G. P. 1939. A biological survey of thirty-one lakes and ponds of the upper Saco River and Sebago Lake drainage systems in Maine. Maine Dept. Inland Fish and Game, Fish Survey Rept. No. 2: 147 p.

Creaser, C. W. 1930. Relative importance of hydrogen-ion concentration, temperature, dissolved oxygen, and carbon-dioxide tension, on habitat selection by brook trout. Ecology 2(2): 246-262.

Duncan, D. B. 1955. Multiple range and multiple F tests. Biometrics, 11: 1-42.

Eipper, A. W. 1960. Managing farm ponds for trout production. Cornell Ext. Bull. 1036, N. Y. State Coll. Agr., 31 p.

Embody, G. C. 1921. Concerning high water temperatures and trout. Trans. Am. Fisheries Soc., 51: 58-64.

__________. 1927. An outline of stream study and the development of a stocking policy. Contr. Agric. Lab. Cornell Univ., 21 p.

Ferguson, R. G. 1958. The preferred temperature of fish and their midsummer distribution in temperate lakes and streams. J. Fish. Res. Bd. Canada, 15(4): 607-624.

Fisher, K. C., and P. Elson. 1950. The selected temperature of Atlantic salmon and speckled trout and the effect of temperature on the response to an electrical stimulus. Physiol. Zool., 23: 28-34.

Fry, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud., Biol. Ser., 55., Publ. Ontario Fish. Res. Lab., 68, 62 p.

Fry, F. E. J., and J. S. Hart. 1948. Cruising speed of goldfish in relation to water temperature. J. Fish. Res. Bd. Canada, 7: 169-175.

Garside, E. T., and J. S. Tait. 1958a. Ontario Dept. of Lands and Forests, Maple, Ontario, Canada, MS.

Garside, E. T., and J. S. Tait. 1958b. Preferred temperature of rainbow trout (Salmo gairdneri) and its unusual relationship to acclimation temperature. Canada J. Zool., 36: 563-567.

Graham, J. M. 1949. Some effects of temperature and oxygen pressure on the metabolism and activity of the speckled trout, Salvelinus fontinalis. Canadian J. Res., 27: 270-288.

Gross, W. L., P. O. Fromm, and E. W. Roelofs. 1963. Relationship between thyroid and growth in green sunfish, Lepomis cyanellus Rafinesque. Trans. Am. Fisheries Soc., 92(4): 401-408.

Hansen, Donald F. 1951. Biology of the white crappie in Illinois. Illinois Nat. Hist. Survey Bull., 25(4): 211-265.

Hatch, Richard W., and D. A. Webster. 1961. Trout production in four central Adirondack Mountain lakes. Mem. 373, N. Y. State Coll. Agr., Agr. Exp. Sta., 81 p.

Hubbs, C. L., and R. W. Eschmeyer. 1938. The improvement of lakes for fishing. Bull. No. 2, Inst. Fisheries Res., Mich. Dept. Conserv., 233 p.

Ivlev, V. S. 1945. The biological productivity of waters. Adv. Mod. Biol., Moscow 19: 98-120. (Translated by W. E. Ricker)

Johnson, W. E., and A. D. Hasler. 1954. Rainbow trout production in dystrophic lakes. J. Wildl. Mgmt. 18(1): 113-135.

Lagler, K. F. 1956. Freshwater fisheries biology. 2nd Ed. Wm. C. Brown Co., Dubuque, Iowa, 421 p.

Leonard, J. W., and F. A. Leonard. 1946. An analysis of the feeding habits of rainbow trout and lake trout in Birch Lake, Cass County, Michigan. Trans. Am. Fisheries Soc., 76: 301-314.

Miller, R. B., and R. C. Thomas. 1956. Alberta's pothole trout fisheries. Trans. Am. Fisheries Soc., 86: 261-268.

Mullan, J. W., and W. A. Tompkins. 1959. Trout pond management in Massachusetts. Publ. Mass. Div. of Fish and Game, 132 p.

Olsen, Sigurd T., and W. H. Marshall. 1952. The common loon in Minnesota. Occas. Paper No. 5, Minn. Mus. Nat. Hist., 77 p.

Ricker, W. E. 1956. Handbook of computations for biological statistics of fish populations. Fish. Res. Bd. Canada, Bull. 119, 300 p.

Ricker, W. E., and R. E. Foerster. 1948. The computation of fish production. Bull. Bingham Oceanog. Coll., 11(4): 173-211.

Roelofs, E. W. 1944. Water soils in relation to lake productivity. Tech. Bull. 190, Mich. State Univ., Agr. Exp. Sta., 31 p.

Rounsefell, G. A. 1958. Anadromy in North American Salmonidae. U. S. Fish and Wildl. Ser., Fish. Bull. 131, 58: 171-185.

Snedecor, G. W. 1956. Statistical methods applied to experiments in agriculture and biology. 5th Ed. The Iowa State College Press, Ames. 534 p.

Tait, J. S. 1958. Temperature preference of the brown trout, Salmo trutta. Ontario Dept. of Lands and Forests, Maple, Ont., MS.

U. S. Department of Agriculture. 1941. The yearbook of agriculture, climate and man. U. S. Govt. Printing Office, Washington, 1248 p.

Veatch, J. O. 1953. Soils and land of Michigan. The Michigan State University Press, East Lansing, 241 p.

APPENDIX A

Sample of Contract Agreement

This Memorandum of Understanding entered into between the FISH DIVISION of the DEPARTMENT OF CONSERVATION of the State of Michigan (The Fish Division) and the LANDOWNER of the lakes listed below (The Landowner) this ____________ day of ____________, 196__.

WITNESSETH:

1. That on the following lakes:

Lake	Location	County
__________________	__________________	____________
__________________	__________________	____________
__________________	__________________	____________

the Fish Division wishes to conduct experimental work on the management of rainbow trout. This study will constitute part of the doctoral research program for ____________ through Michigan State University.

2. The purpose of this experimental work is to obtain technical information relative to the survival and growth of planted rainbow trout in a selected series of warm water lakes of varying physical, chemical, and biological characteristics.

3. The general plan of the study is:

   A. Eliminate the fish population in each lake with a fish toxicant.

B. Plant approximately ___ legal and ___ fingerling rainbow trout per acre in each lake prior to ____________________, 196_.

C. At frequent intervals run temperature-chemical profile analysis, and test net to obtain data on survival and growth of the planted fish.

D. Other observations on the habits of the trout will be made as time permits.

E. All fish removed from each lake by angling will be recorded by the exact length and date of capture.

F. Each lake will be re-treated approximately ________________, 196_, with a chemical toxicant to obtain final production data.

G. During the calendar year following completion of items A through F above, the Fish Division will repeat the trout plant of approximately ___ legals and ___ fingerling rainbow trout per acre or at the Landowners option plant instead 100 fingerling bass and 500 fingerling bluegills each per acre of each lake. Any changes from the above planting must be agreed to in writing with the Fish Division before March 1 of the Calendar year. This plant of fish is considered part of the study and test net survival and growth checks will be made by Fish Division personnel as necessary until the termination of this Memorandum of Understanding, at that time the stock of fish will become the property of the Landowner in lieu of the original stock of fish at the initiation of the study.

4. As his contribution to the above study, the Landowner agrees to:

A. Furnish free access to the above named lakes during the period of study to personnel of the Fish Division engaged in the study.

B. Furnish the Fish Division a complete record monthly of all fish removed by angling on the forms provided.

C. Limit the amount of fishing effort to assure a working stock of trout in each lake during the course of the study.

5. As its part in the above study, the Fish Division through its representatives agrees to:

A. Furnish and apply all necessary chemical fish toxicants.

B. Furnish and plant the prescribed stocks of fish.

C. Conduct the field investigations in a thorough and scientific manner.

D. Process the creel census information taken by the Landowner.

E. Furnish the Landowner a summary report of the experimental findings on each lake.

6. This Memorandum of Understanding will terminate __________ ____________________________, 196__.

IN WITNESS WHEREOF, the parties hereto have set their hands.

DEPARTMENT OF CONSERVATION
OF THE STATE OF MICHIGAN

By ____________________________________

Title __________________________________

PROPERTY OWNER, OR QUALIFIED
REPRESENTATIVE

By ____________________________________

Title __________________________________

APPENDIX B

Temperature, oxygen, and other water chemistry

data for the ten experimental lakes, 1960

Table 26. Water chemistry profiles of Bass Lake, Clare County, on April 28, 1960 and August 10, 1960

Depth (meters)	April 28, 1960 Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*	August 10, 1960 Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*
0	56.3	--	-	--	--	--	70.4	--	-	--	--	--
1	55.1	9.8	0	90	tr	8.2	70.4	7.2	3	98	0	8.5
2	52.8	10.6	0	93	tr	8.2	70.3	7.1	3	98	0	8.5
3	43.7	11.3	0	98	0	8.2	69.4	6.8	2	98	0	8.5
4	41.6	9.6	0	100	1	8.1	61.1	7.2	0	100	2	8.2
5	40.4	5.0	0	109	4	8.0	51.4	1.5	0	106	3	8.0
6	40.3	1.4	0	111	7	7.6	45.3	1.2	0	110	5	7.9
7	39.6	0.3	0	119	7	7.6	42.0	0.0	0	129	8	7.6
8	39.5	0.0	0	135	11	7.4	40.4	0.0	0	132	9	7.5
9	39.4	0.0	0	137	12	7.3	40.0	0.0	0	137	10	7.4
10	39.4	0.0	0	137	14	7.2	40.0	0.0	0	--	--	--
11	39.4	0.0	0	137	14	7.2	40.0	0.0	0	--	--	--
12	39.4	--	-	--	--	--	--	--	-	--	--	--
13	39.5	--	-	--	--	--	--	--	-	--	--	--

*pH some difficulty occurred in calibration for field measurements with the pocket Beckman pH meter--results are only approximate.

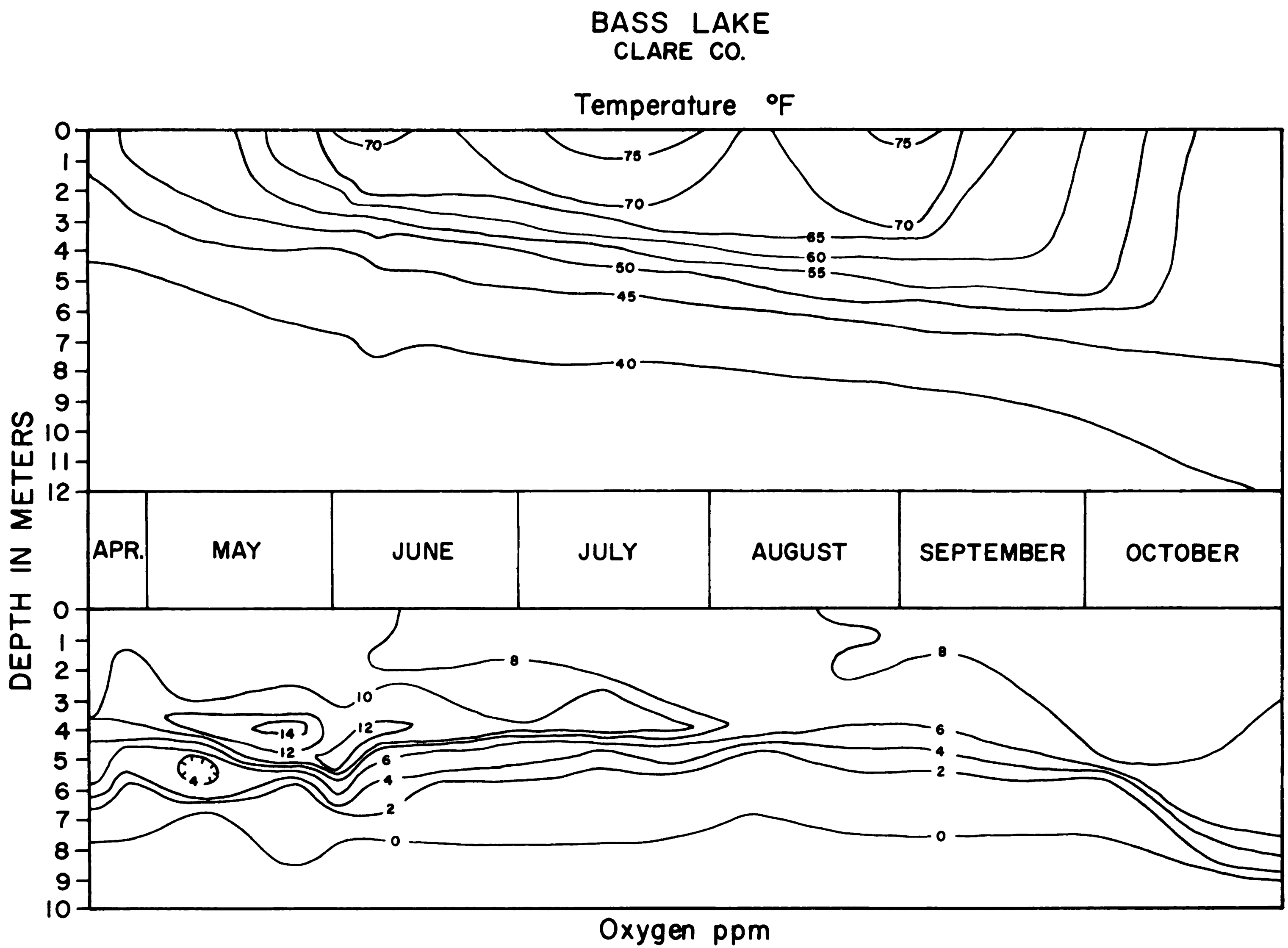


Fig. 25. Temperature and oxygen record for Bass Lake, 1960.

Table 27. Water chemistry profiles of Doyle Lake, Roscommon County, on April 26, 1960 and August 8, 1960

Depth (meters)	April 26, 1960						August 8, 1960					
	Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M. O. (ppm)	CO_2 (ppm)	pH*	Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M. O. (ppm)	CO_2 (ppm)	pH*
0	55.0	--	-	--	--	--	70.0	--	-	--	--	--
1	55.0	9.4	0	70	1	8.1	70.1	7.5	1	68	0	8.4
2	55.0	9.4	0	70	1	8.0	69.9	7.5	1	68	0	8.4
3	51.3	9.3	0	70	1	7.9	69.9	7.4	1	68	0	8.3
4	44.0	8.0	0	74	3	7.9	64.5	6.9	0	70	tr	8.2
5	42.4	5.6	0	79	3	7.9	59.0	3.5	0	70	1	8.0
6	41.1	5.5	0	80	5	7.7	52.6	3.6	0	70	1	7.9
7	41.1	4.5	0	81	5	7.4	49.2	3.9	0	75	1	7.9
8	41.2	--	-	--	--	--	48.6	--	-	--	--	--

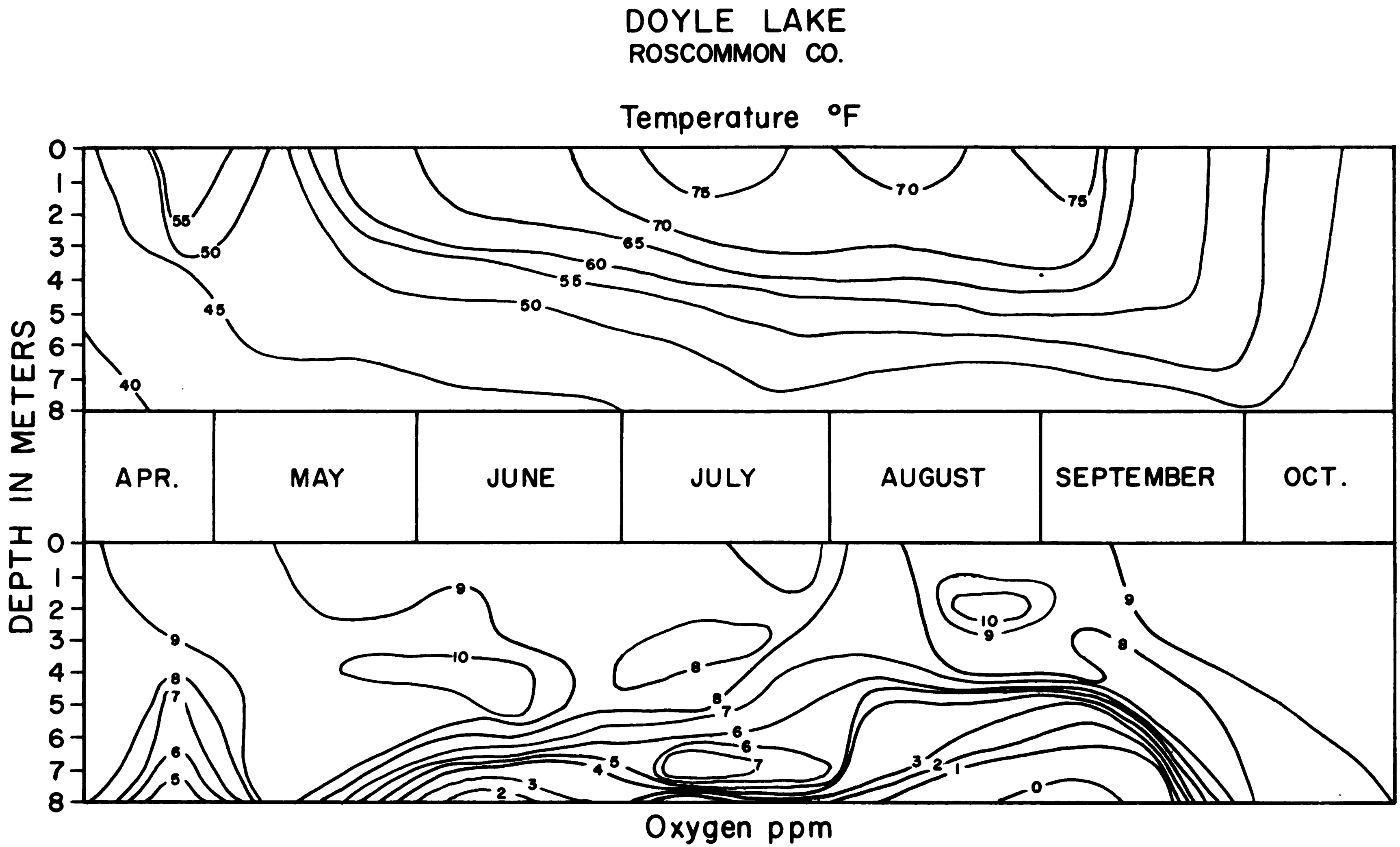


Fig. 26. Temperature and oxygen record for Doyle Lake, 1960.

Table 28. Water chemistry profiles of South Twin Lake, Mecosta County, on April 28, 1960 and August 9, 1960

Depth (meters)	April 28, 1960 Temp. (° F)	O₂ (ppm)	ph-th (ppm)	M. O. (ppm)	CO_2 (ppm)	pH*	August 9, 1960 Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M. O. (ppm)	CO_2 (ppm)	pH*
0	--	--	-	--	--	--	70.1	--	-	--	--	--
1	55.2	8.9	0	139	2	8.0	69.8	8.4	0[1]	129	1	8.2
2	54.9	7.9	0	144	2	8.0	67.1	8.4	0	131	1	8.2
3	49.0	7.5	0	162	5	7.8	55.7	8.4	0	149	5	7.8
4	41.6	7.5	0	163	5	7.8	48.0	0.5	0	167	10	7.6
5	40.0	7.5	0	172	5	7.6	43.2	0.0	0	190	12	7.4
6	40.0	7.5	0	173	8	7.5	41.0	0.0	0	208	12	7.4
7	40.0	6.3	0	192	8	7.4	40.2	0.0	0	212	13	7.4
8	40.2	6.3	0	204	12	7.3	40.2	0.0	0	218	15	7.4

[1]Algae bloom on August 3 (O_2 = 14.8 ppm, ph-th = 5).

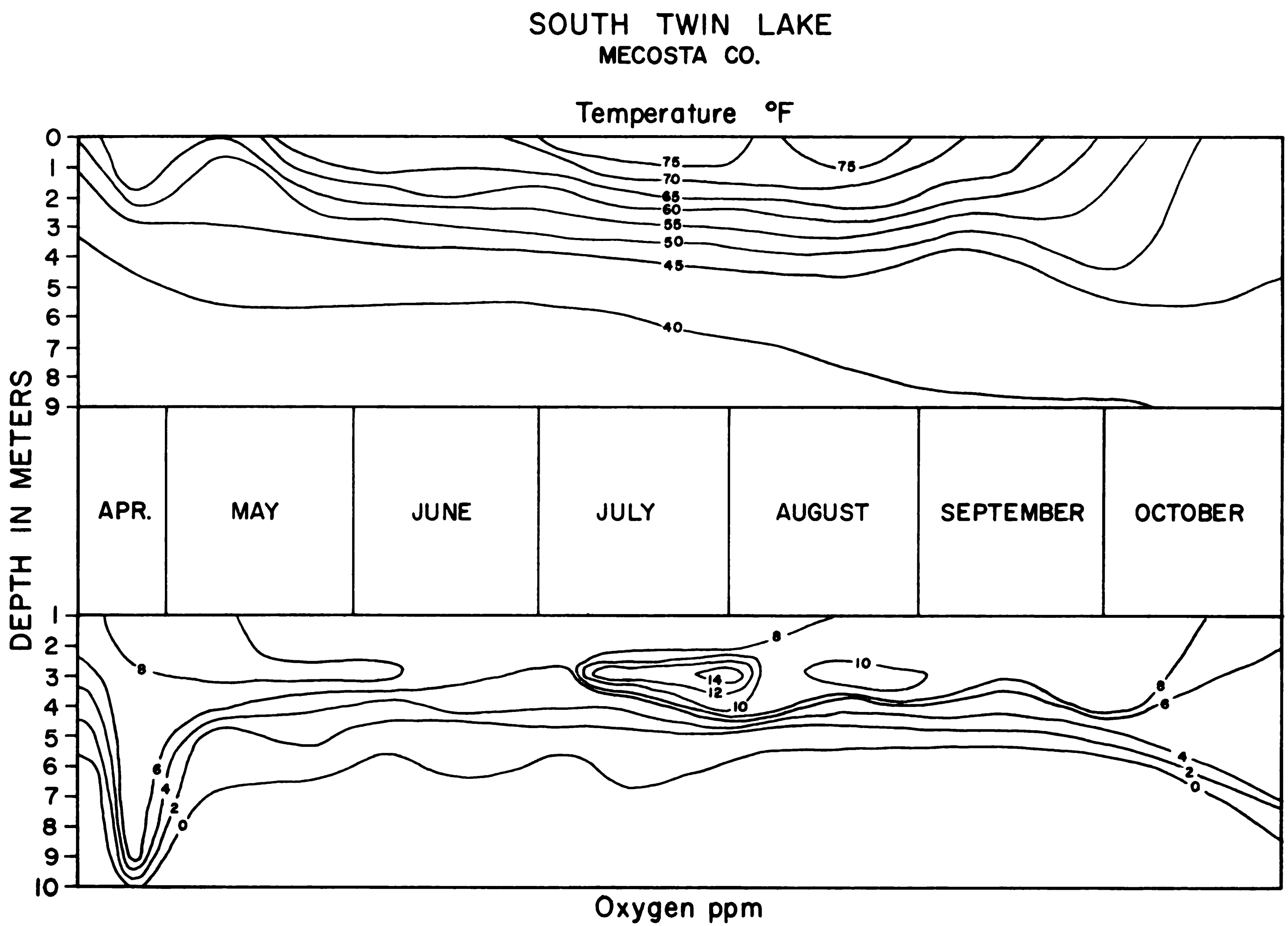


Fig. 27. Temperature and oxygen record for South Twin Lake, 1960.

Table 29. Water chemistry profiles of North Twin Lake, Mecosta County, on April 28, 1960 and August 9, 1960

Depth (meters)	April 28, 1960 Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*	August 9, 1960 Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*
0	56.0	--	-	--	--	--	72.0[1]	8.7	15	127[1]	0	8.9
1	55.8	17.6	33	102	0	9.6	70.5	7.0	7	138	0	8.9
2	53.0	16.5	27	102	0	9.4	69.9	3.2	0	139	tr	8.2
3	42.0	4.5	0	154	1	8.2	67.7	0.1	0	156	4	8.0
4	40.0	tr	0	190	5	8.0	58.2	0.0	0	175	7	7.8
5	40.0	0.0	0	235	30	7.5	50.8	0.0	0	200	12	7.6
6	40.1	0.0	0	274	45	7.5	46.2	0.0	0	265	40	7.5
7	40.3	0.0	0	317	60	7.5	44.2	0.0	0	296	45	7.2
8	40.5	0.0	0	336	75	7.0	44.2	--	-	--	--	--

[1]Temperature and M.O. alkalinity affected by artificial circulation with compressed air in June and July.

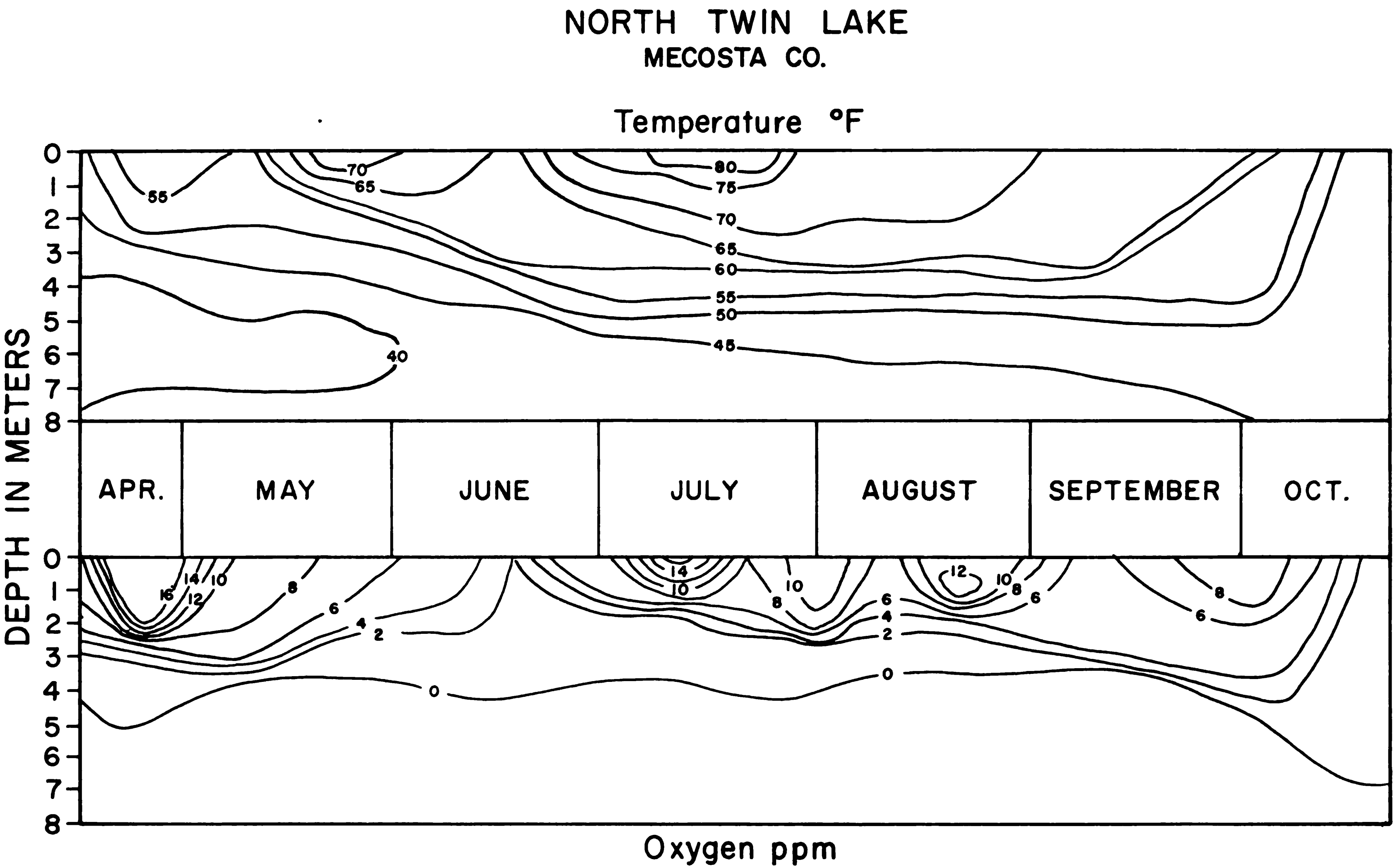


Fig. 28. Temperature and oxygen record for North Twin Lake, 1960.

Table 30. Water chemistry profiles of Ryan Lake, Roscommon County, on April 26, 1960 and August 9, 1960

Depth (meters)	April 26, 1960 Temp. (° F)	O$_2$ (ppm)	ph-th (ppm)	M.O. (ppm)	CO$_2$ (ppm)	pH*	August 9, 1960 Temp. (° F)	O$_2$ (ppm)	ph-th (ppm)	M.O. (ppm)	CO$_2$ (ppm)	pH*
0	53.9	--	-	--	--	--	69.3	--	-	--	--	--
1	53.9	8.4	0	60	2	7.9	69.5	7.4	0	80	1	8.0
2	53.9	8.4	0	60	3	7.8	69.5	7.3	0	75	1	8.0
3	49.6	8.1	0	58	3	7.8	65.4	6.0	0	66	2	7.9
4	46.5	8.0	0	58	3	7.8	55.6	1.2	0	60	3	7.8
5	44.3	7.3	0	58	3	7.8	50.0	1.0	0	57	5	7.7
6	42.0	6.1	0	58	5	7.7	47.6	--	-	--	--	--

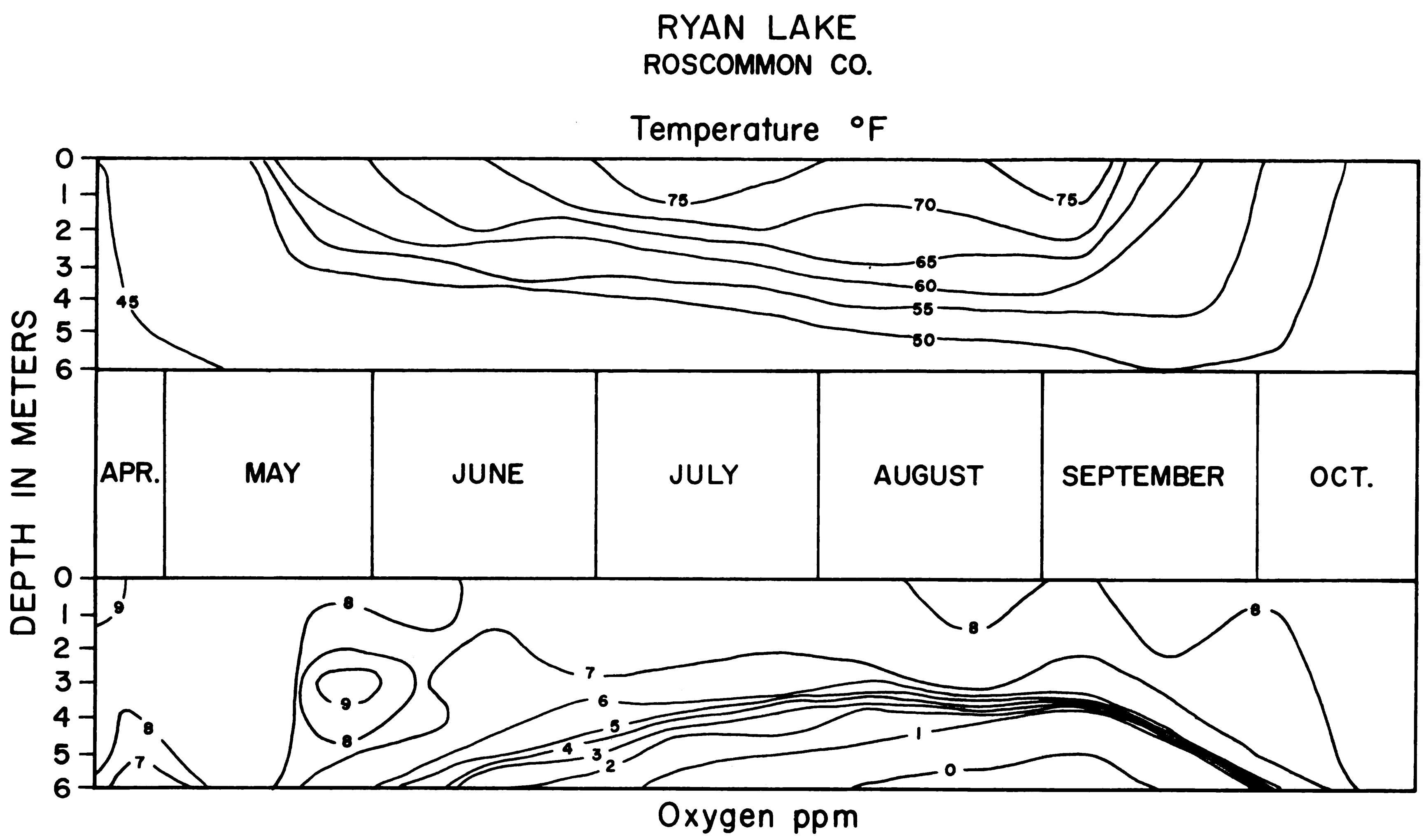


Fig. 29. Temperature and oxygen record for Ryan Lake, 1960.

Table 31. Water chemistry profiles of Norway Lake, Clare County, on April 28, 1960 and August 10, 1960

Depth (meters)	April 28, 1960						August 10, 1960					
	Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M. O. (ppm)	CO_2 (ppm)	pH*	Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M. O. (ppm)	CO_2 (ppm)	pH*
0	56.4	--	-	--	--	--	69.5	--	-	--	--	--
1	56.4	15.3	8	8	0	10.0	69.5	9.9	3	13	0	9.9
2	53.2	14.5	5	11	0	9.9	68.4	9.9	3	13	0	9.9
3	44.8	12.0	1	16	0	8.4	51.7	8.6	0	17	1	8.2
4	41.2	2.5	0	16	tr	8.0	44.3	1.7	0	25	6	7.7
5	40.2	--	-	--	--	--	42.0	--	-	--	--	--

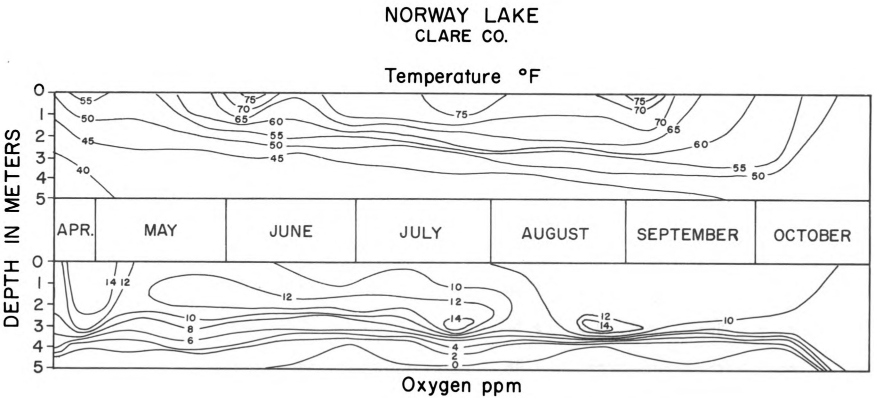


Fig. 30. Temperature and oxygen record for Norway Lake, 1960.

Table 32. Water chemistry profiles of Little Lake, Roscommon County, on April 26, 1960 and August 9, 1960

Depth (meters)	April 26, 1960						August 9, 1960					
	Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*	Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*
0	54.0	--	-	--	--	--	69.2	--	-	--	--	--
1	52.1	7.7	0	21	3	7.6	69.3	4.8	0	19	1	7.2
2	44.2	5.6	0	21	5+	7.6	69.3	4.8	0	20	2	7.2
3	41.8	2.4	0	25	7+	7.5	60.4	0.5	0	21	4	7.0
4	41.2	0.6	0	30	21	7.5	52.4	0.0	0	38	6	6.8
5	41.7	--	-	--	--	--	48.7	--	-	--	--	--

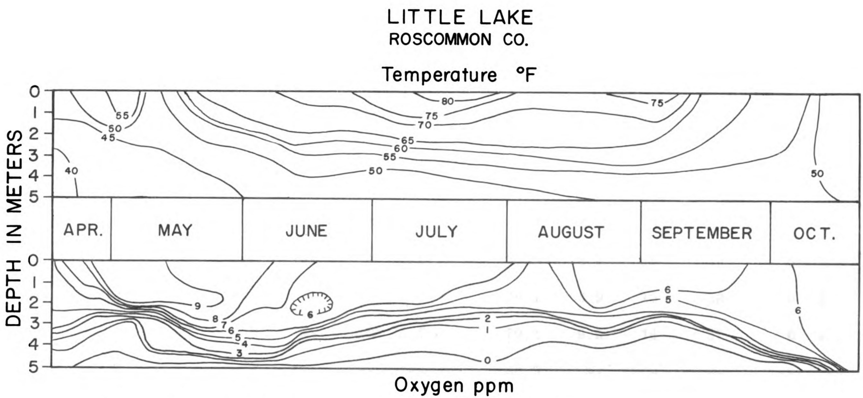


Fig. 31. Temperature and oxygen record for Little Lake, 1960.

Table 33. Water chemistry profiles of Slide Lake, Roscommon County, on April 26, 1960 and August 9, 1960

Depth (meters)	April 26, 1960 Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*	August 9, 1960 Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*
0	54.2	--	-	--	--	--	70.5	--	-	--	--	--
1	54.2	11.5	0	93	0	8.2	70.4	8.8	14	58	0	9.0
2	52.6	11.5	0	94	0	8.2	70.3	8.9	15	58	0	9.1
3	47.0	11.7	0	94	0	8.2	70.1	8.9	16	58	0	9.1
4	46.6	13.5	1	94	0	8.3	70.1	9.0	14	57	0	9.1
5	45.6	--	-	--	--	--	68.5	--	-	--	--	--

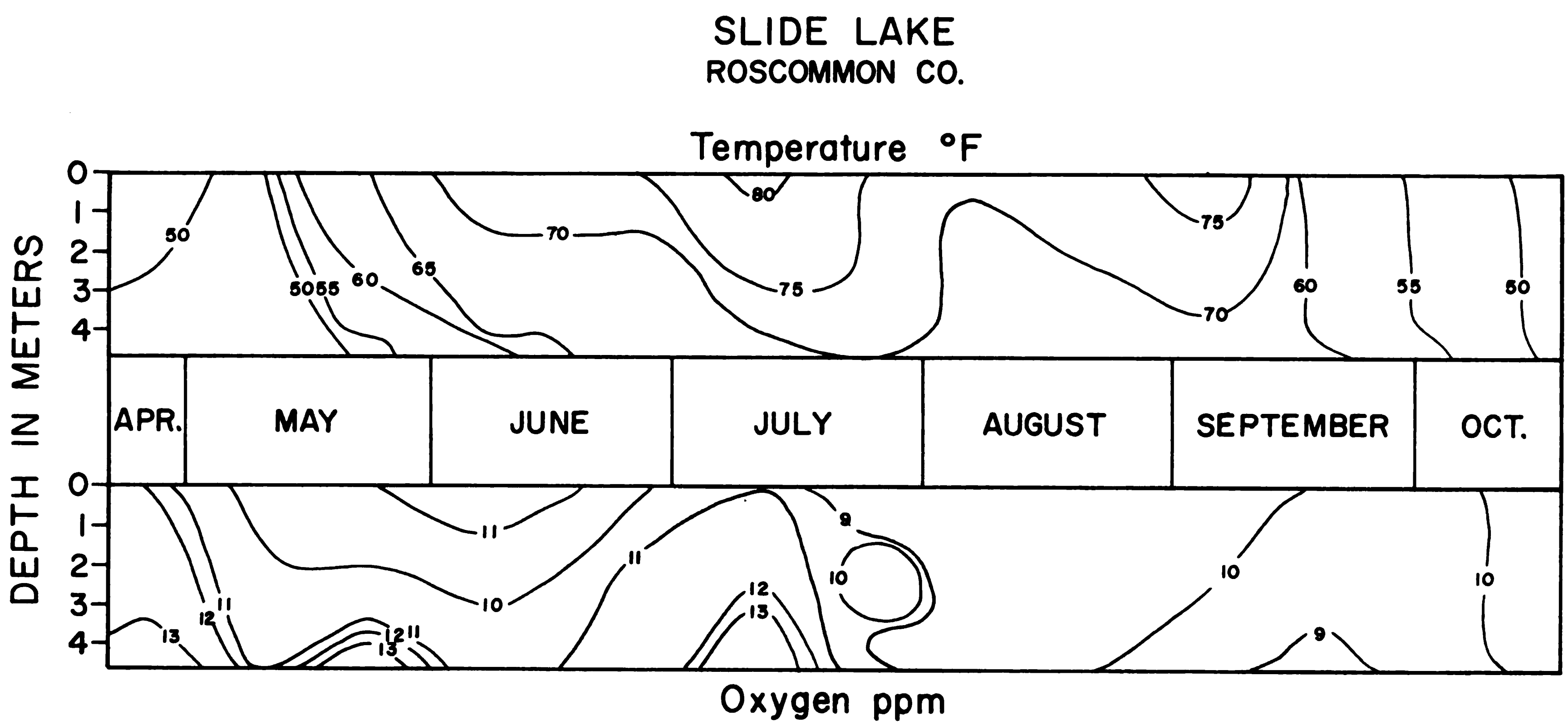


Fig. 32. Temperature and oxygen record for Slide Lake, 1960.

Table 34. Water chemistry profiles of Little Headquarters Lake, Roscommon County, on April 26, 1960 and August 9, 1960

Depth (meters)	April 26, 1960						August 9, 1960					
	Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*	Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*
0	54.5	--	-	--	--	--	70.4	--	-	--	--	--
1	54.4	10.0	0	78	0	8.2	70.4	8.9	12	40	0	9.0
2	52.0	10.4	0	78	0	8.2	70.4	8.8	12	40	0	9.0
3	49.2	11.2	0	76	0	8.2	70.4	8.9	13	40	0	9.0
4	48.9	--	-	--	--	--	70.2	--	-	--	--	--

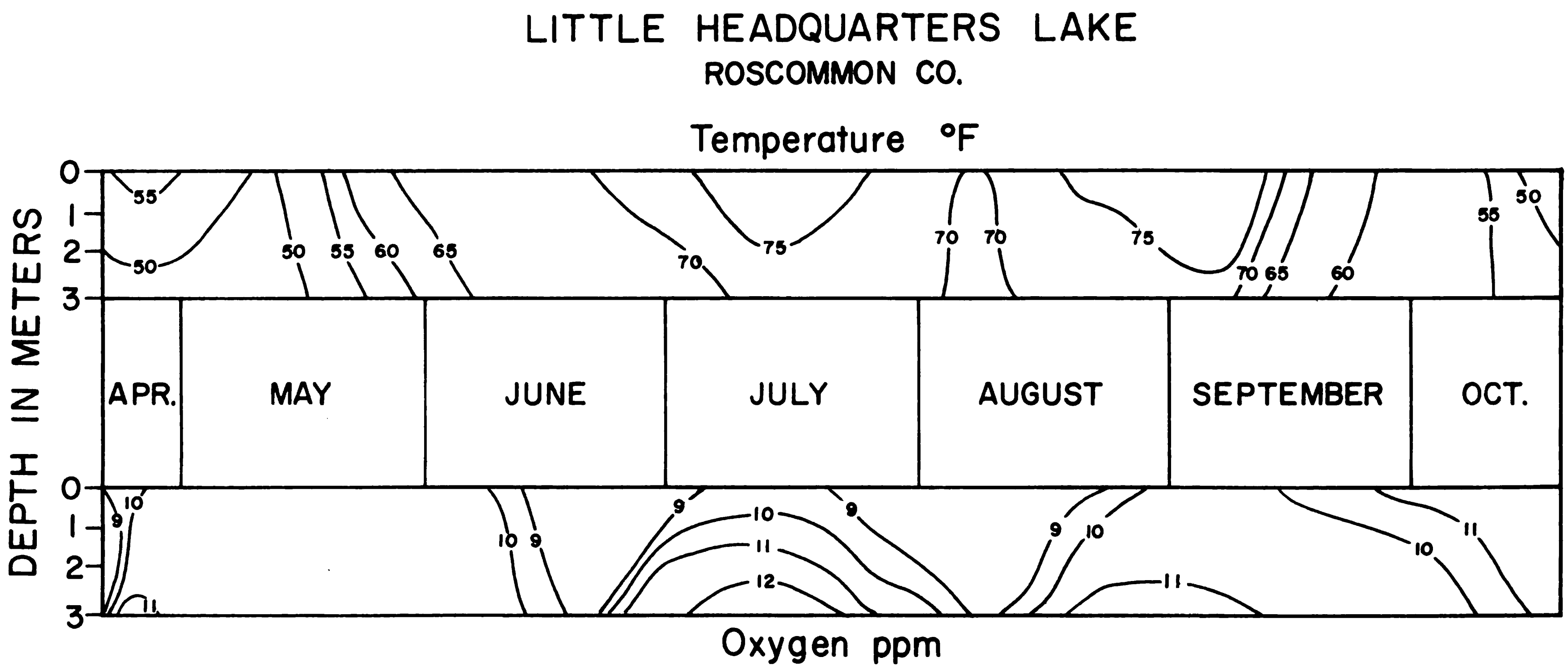


Fig. 33. Temperature and oxygen record for Little Headquarters Lake, 1960.

Table 35. Water chemistry profiles of Marl Lake, Roscommon County, on April 26, 1960 and August 9, 1960

Depth (meters)	April 26, 1960						August 9, 1960					
	Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*	Temp. (° F)	O_2 (ppm)	ph-th (ppm)	M.O. (ppm)	CO_2 (ppm)	pH*
0	56.4	--	-	--	--	--	70.1	--	-	--	--	--
1	56.4	9.1	0	47	0	8.1	70.1	8.3	4	42	0	8.8
2	54.1	9.1	0	47	0	8.1	70.1	8.4	4	42	0	8.8
3	48.7	10.3	0	45	0	8.2	70.0	8.4	4	42	0	8.8

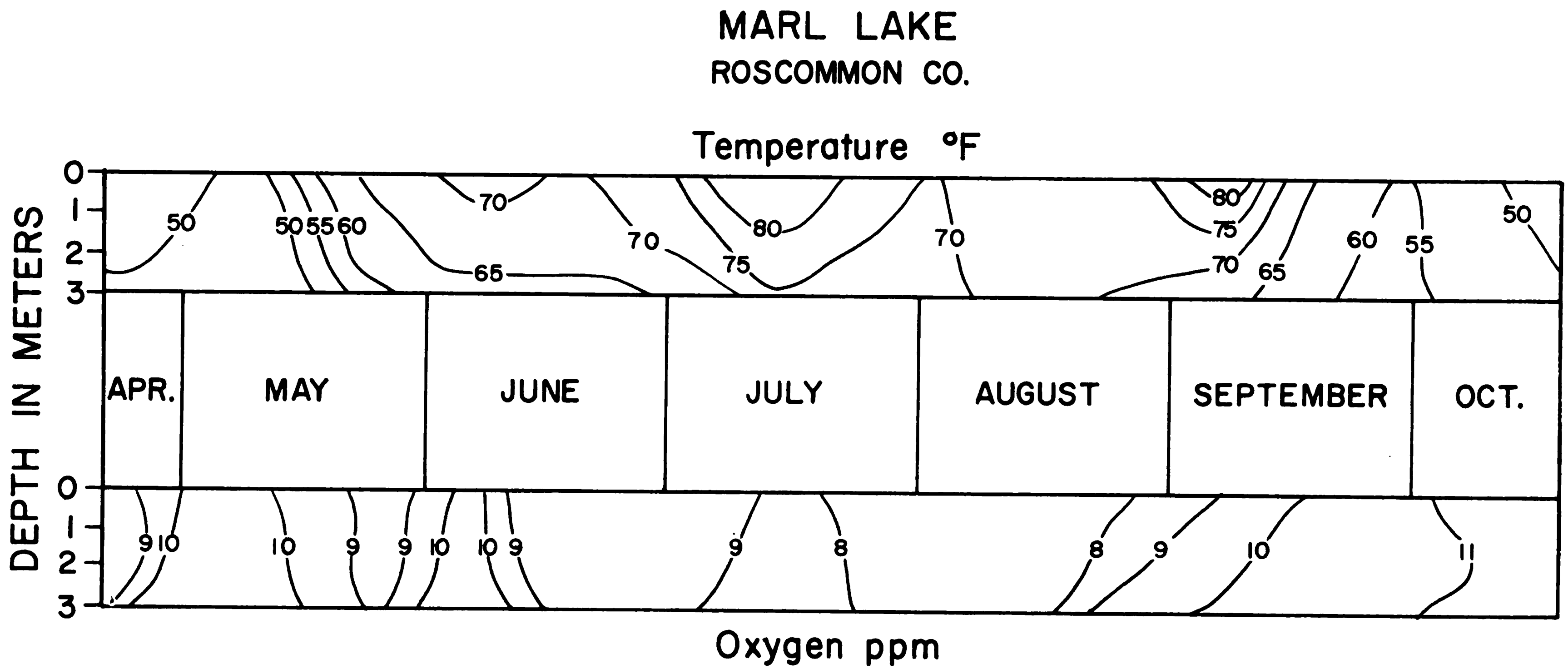


Fig. 34. Temperature and oxygen record for Marl Lake, 1960

APPENDIX C

Names of fishes cited in the text[1]

Common name	Scientific name
Rainbow trout	*Salmo gairdneri* Richardson
Brown trout	*Salmo trutta* Linnaeus
Brook trout	*Salvelinus fontinalis* (Mitchill)
Central mudminnow	*Umbra limi* (Kirtland)
Northern pike	*Esox lucius* Linnaeus
Northern redbelly dace	*Chrosomus eos* Cope
Golden shiner	*Notemigonus crysoleucas* (Mitchill)
Common shiner	*Notropis cornutus* (Mitchill)
Creek chub	*Semotilus atromaculatus* (Mitchill)
White sucker	*Catostomus commersoni* (Lacepede)
Black bullhead	*Ictalurus melas* (Rafinesque)
Yellow bullhead	*Ictalurus natalis* (Le Sueur)
Brown bullhead	*Ictalurus nebulosus* (Le Sueur)
Brook stickleback	*Eucalia inconstans* (Kirtland)
Green sunfish	*Lepomis cyanellus* (Rafinesque)
Pumpkinseed	*Lepomis gibbosus* (Linnaeus)
Largemouth bass	*Micropterus salmoides* (Lacepede)
Black crappie	*Pomoxis nigromaculatus* (Le Sueur)
Johnny darter	*Etheostoma nigrum* Rafinesque
Yellow perch	*Perca flavescens* (Mitchill)

[1] cf. American Fisheries Society, 1960. A list of common and scientific names of fishes from the United States and Canada. 2nd Ed. Spec. Publ. No. 2, Am. Fisheries Soc., 102 p.