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EDWIN JOHN CROSSMAN

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FACTORS INVOLVED IN THE PREDATOR-PREY RELATIONSHIP OF RAINBOW TROUT (*Salmo gairdneri* Richardson) AND REDSIDE SHINERS [*Richardsonius balteatus* (Richardson)] IN PAUL LAKE, BRITISH COLUMBIA

ABSTRACT

The role of such factors as distribution and movements of predator (*Salmo gairdneri*) and prey (*Richardsonius balteatus*), the activity involved in predation and the contribution of prey to the diet of the predator were studied in order to answer where, when, how and to what extent trout preyed on shiners.

Data for 1955 and 1956 are compared with data for years when trout alone inhabited the lake. Predation became significant in 1950, approximately five years after the introduction of the prey species and has increased steadily, especially in trout over 10 inches in length, since that time.

Movements of shiners in Paul Lake are complex and tend to bring this species into contact with trout during July, August and September. At this time shiners constitute over 90 percent of the diet of trout over 14 inches in length and lesser volumes in smaller trout. Trout under six inches in length prey on shiners to an insignificant degree. In winter shiners form a negligible part of the diet of trout of all sizes. Movement patterns seem to indicate that these two species might be separated in winter, and as a result predation is almost nil.

It is inferred from the study that predation by trout is not a control of the number of shiners in the lake.

The growth rate of trout under eight inches in length is still depressed as a result of competition with shiners for food. The contribution of shiners through predation, to the diet of larger trout, appears to have elevated the growth rate of trout eight to twelve inches in length, somewhat above that for years when trout alone inhabited the lake.

The casual rather than causative nature of this predator-prey interaction is compared with the more stylized, obligate relationships of predator and prey in models of predation in the published literature. This relationship between rainbow trout and redside shiners is also discussed as it applies to management of lakes in which "sport fish" and "coarse fish" coexist.

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FACTORS INVOLVED IN THE PREDATOR-PREY RELATIONSHIP OF RAINBOW TROUT (*Salmo gairdneri* Richardson) AND REDSIDE SHINERS (*Richardsonius balteatus* (Richardson)) IN PAUL LAKE, BRITISH COLUMBIA.

by

EDWIN JOHN CROSSMAN

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE
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Date September 21, 1957

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Unpublished data, from a study carried out on Paul Lake in 1952, was made available by the B.C. Game Commission and was utilized in the section on distribution and movements of predator and prey.

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INTRODUCTION

Predator-prey relationships, of the type which imply that one animal is killed by another and consumed as food, are common in freshwater fish. Clemens et al, (1923) in a study of the food of Lake Nipigon fishes classified the fish into five categories on the basis of food habits. The first category dealt with was predacious fish, those whose food is primarily other fish. Volterra (1928) claimed that "since among fish there were species that ate one another," these animals seemed the most likely to provide verification, under natural conditions, of laws he proposed to explain the fluctuations in the number of animal species living together. Ricker (1952) divided predation into three types, which deal with the number of prey consumed by predators in three different "situations." He cited several fish species-combinations, as examples of the type of predation in two of these situations. It would appear then, that one animal attacking and consuming another is, as a means of procuring food, widely distributed among fish.

While this type of activity is widely distributed among fish, the factors governing it are not well known. Larkin (1956) reviewing interspecific competition mentions the scarcity of literature on, and lack of clear understanding of, the two phenomena, predation and competition, among freshwater fish populations. Often predation is confused with, or included in, the more embracing term competition. Canibalism in fish is, at the same time, referred to as an effect of competition and as a special type of predation. Nicholson (1933) and Nicholson and Bailey (1935) use both the terms interspecific competition and predation to describe the searching of an entomophagus parasite for a host. Lagler (1944) states that the distinction between competition and predation is not so clear cut as may be inferred since predation is actually competition for survival. Attempts to follow predator-prey interactions and to describe the factors involved in this association would help to clarify any differences in these phenomena.

This interaction of predator and prey has long been considered of major significance in the management of various stocks of commercial and sport fish. Clemens (1934) deals with the problem of certain fish, such as cutthroat trout (Salmo clarki Richardson) and steelhead (Salmo gairdneri Richardson), being considered both as predators on commercially important salmon (Oncorhynchus) and as economically important sport fish. Ricker (1941) and Foerster and Ricker (1942) discuss the effects of reduction of predacious fish on the production of sockeye salmon (Oncorhynchus nerka (Walbaum)). The principal predators were squawfish (Ptychocheilus oregonense (Richardson)), Dolly Varden char (Salvelinus alpinus malma (Walbaum)), trout (Salmo gairdneri Richardson) and coho salmon (Oncorhynchus kisutch (Walbaum)). These writers were able to reduce squawfish and char to one-tenth of their former numbers but they state that the abundance of trout and coho salmon may not have been affected at all. This reduction of the former two species may have led to an increase in the latter two and no actual reduction in predation. Swingle (1950) describes the effects of predator-prey relationships on population balance in pond management. He had, however, maximum control of population numbers and relative numbers of species in the ponds. Even then the ponds had to be drained at times in order to kill off excesses in one or the other species which threatened to destroy the balance. These situations, while illustrating the importance of the consideration of predator-prey relationships, also point up the complications involved in attempting to study and manipulate combinations of prey and several predators, or one predator and several prey. Under these circumstances, factors of competition for food and space and factors of predation are so interdependent as to make segregation almost impossible.

As shown above studies of predator-prey interactions are usually complicated by the presence of many species in a single body of water. Paul Lake, British Columbia, however, affords an opportunity to study the phenomenon of predation with a minimum of complicating elements. It contains only two species of fish. While these two species have interchanging roles in the predator-prey complex, the more pronounced situation is that in which the rainbow trout (Salmo gairdneri Richardson) is the predator and the redside shiner (Richardsonius balteatus (Richardson)) is the prey. It is this predator-prey relationship which will be dealt with in the study to be outlined below.

The simplicity of the situation in this lake, as it applies to a study of predation, is surpassed only by that in fish ponds. The limited area of the ponds and the somewhat unnatural environment makes studies of predation in them of limited value. Paul Lake constitutes a natural habitat in which to study predator and prey, to describe the facets of the interaction between these two fish and to delimit some of the factors governing the interaction.

The practical value of a study of this type is in its application to the management of sport fishing in a lake such as Paul Lake. It makes available information concerning the effect, on trout, of shiners as competitors and as food. The scientific value of the study lies in the description of the factors involved in predator-prey relationship. The simplicity of the faunal complex in the lake and the long and well-documented history of the lake enables one to follow the development of predacious food habits in a population of rainbow trout. The presence of only two species makes possible at least partial separation of the factors governing the interaction between predator and prey. Any description of these factors may be useful in a critical examination of the mathematical models constructed to describe predation by such authors as Lotka (1925), Volterra (1928), Nicholson (1933), and Nicholson and Bailey (1935).

It is apparent that predator-prey associations embody important considerations both in the study and management of fish. This is especially true in the case of freshwater fish. There is a need for precise description of actual predator-prey situations and a need to clarify the distinction between predation and competition. Mathematical presentations of these interactions stimulate thought and broad areas of research. It is possible, on the other hand, while dealing mainly with numbers of fish involved, birth rates, death rates and reproductive potential, the mathematical approach neglects the effects of factors involved in reaction of individuals and reaction to environment. These characteristics, that is those not strictly related to relative numbers of predator and prey, possibly create different interactions in even nearly similar environmental situations. Some of these density independent factors such as distribution and movement of predator, movement of prey in response to temperature and behaviour of predator will be dealt with in the discussion below.

DESCRIPTION OF STUDY SITE

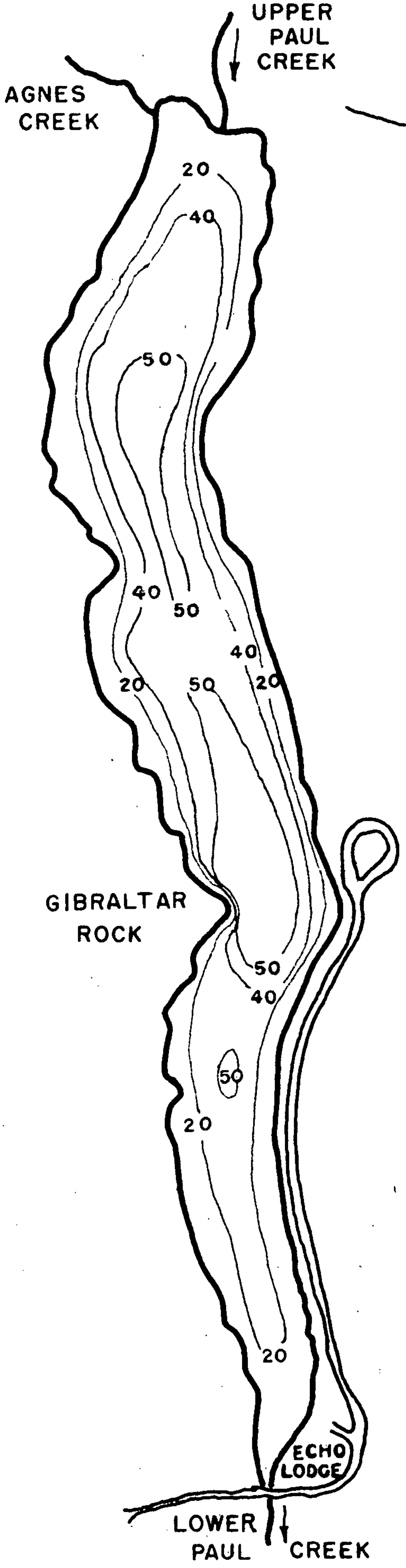
Paul Lake is situated 12 miles north-east of Kamloops, British Columbia, at an altitude of 2,542 feet. Larkin et al (1950) have described the physical features of the lake. It has a length of 3.8 miles and an average width of 0.3 miles. The area of the lake is approximately 1.5 square miles or 960 surface acres, shore development is 5.55 units, maximum depth is 55.5 metres (182 feet) and approximately 33 percent of the area lies below the 50 metre contour (see Figure 1). The mean depth is 34.2 metres (112 feet) and the greater portion of the shore slopes off at an angle of from 20 to 25 degrees. There is one major inlet, Upper Paul Creek, which drains Pinantan Lake, and a few mountain streams entering the lake which become dry in the summer months. The outlet, Lower Paul Creek, which joins the North Thompson river, is screened and water is stored in the lake by means of a dam. The outlet flows almost continuously in summer as some of the outflow is used for irrigation.

Physical and chemical properties of the lake are extensively described by Rawson (1934) and Larkin et al (1950). These authors and various papers by C. McC. Mottley (between 1931 and 1941) summarize the fauna and ecology of the lake from 1931 to 1949.

Mottley (1932) describes the sequence of events from the original liberation of 5000 rainbow trout fry in 1909. There was a rapid build-up, by 1920, of a large, underexploited population. Efficient utilization of food by this large population led to a decrease in size of trout (e.g. average weight of mature trout in 1922 was four pounds while in 1925 it was two pounds). The building of a good road to Paul Lake in 1924 led to increased angling pressure, and size of trout increased gradually to a maximum weight of nine pounds in 1931. By 1931 however, a decrease in total catch, catch per unit of effort and number of trout in the spawning run, indicated a condition of depletion.

To compensate for loss of production in the spawning stream Mottley, in 1932, suggested stocking the lake annually with 200,000 fry. Mottley (1940) reported that by 1937, even in the face of increased angling pressure, total catch was remaining stable between 9,000 and 10,000 fish per year or an average crop of approximately 10 pounds per acre. This figure he took as a measure of the lake's optimum productivity. Larkin et al (1950) report that this rate of production continued to 1949 (see Table I). Up to this time yearling and two-year-old trout constituted approximately 68 percent of the anglers' catch.

Larkin and Smith (1954) report that in approximately 1945 the redside shiner made its way into Paul Lake from lakes above it in the chain into which it had been artificially introduced at an earlier date. Shiners competed with



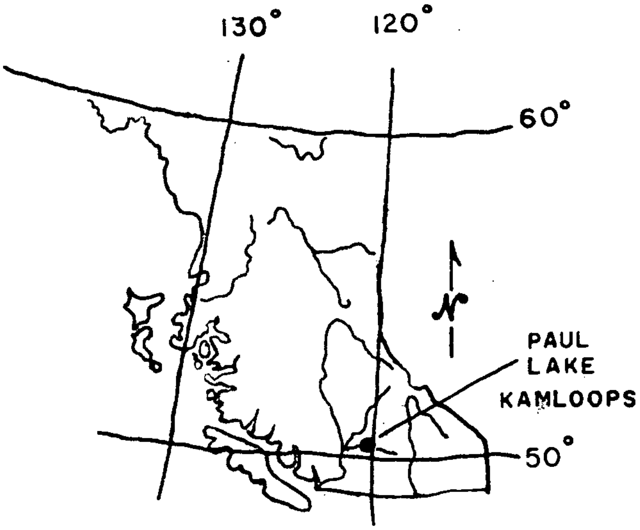


Fig. 1. Paul Lake showing depth contours, streams and access road.

Inset shows approximate location in province of British Columbia.

TABLE I

Fluctuation in Anglers' Catch of trout in Paul Lake
1932 - 1955

YEAR	TOTAL CATCH OF TROUT	CATCH PER BOAT DAY	AVERAGE WEIGHT
1932	3,000	4	1.49
1936	10,000	9	1.00
1949	11,000	3.7	1.01
1954	2,349	2.1	1.0 (est.)
1955	10,043	4.3	1.0 (est.)

One boat day is equivalent to 10 hours fishing.

Figures for 1932-1949 from Larkin et al (1950).

Figures for 1954 and 1955 from Smith (1955).

trout for food and space and large shiners preyed on trout fry. Interaction of these two species resulted in a drop in the population of trout and a decreased growth rate of trout. This decrease in growth rate subjected the trout to further seasons of natural mortality before they were catchable size. Between 1948 and 1954 the total annual catch in Paul Lake declined from an average of 10,000 trout to less than 2,400 (partly attributable to fewer anglers). By 1953 and 1954 two, three and four year-old fish were the bulk of the catch. Few yearlings grew large enough to enter the fishery.

A research programme on Paul Lake in 1952 led to the decision to stock the lake with yearling trout and to suspend egg taking in Upper Paul Creek. By raising trout beyond the size range in which they were most affected by competition for food from shiners, and to a size from which they would soon grow into predators on shiners, it was hoped that angling would be rehabilitated.

In September 1953 the lake was stocked with 10,000 fall fingerlings (approx. 600/lb.) in addition to the annual liberation of 50,000 fry. From 1954-1957 inclusive the lake was stocked, in the spring, with marked yearling trout (approx. 40/lb. 3-4 in.) and no fry were liberated.

In 1955 a study programme was initiated through the Institute of Fisheries, University of British Columbia, and financed by the British Columbia Game Commission. The project was primarily concerned with the continuing investigation of interaction between rainbow trout and redside shiners in Paul Lake, including assessment of:-

1. Competition between trout and shiners for food.
2. Predation by shiners on small trout.
3. Predation by trout on shiners.

The present study deals with the third facet of the interaction, in which several notable changes have occurred in recent years.

Predation by trout on shiners has been increasing each year. Larkin and

Smith (1954) state that no shiners were seen in the stomachs of trout until 1950, approximately five years after the introduction of this species into Paul Lake. Larkin et al (1950) state that a similar time lapse may have occurred in Pinantan and Hyas lakes from which the shiners entered Paul Lake. These authors note that according to local reports it was three or four years after the introduction of shiners into Hyas and Pinantan lakes, that trout were first observed to have eaten them.

Prior to 1950 all sizes of trout utilized the same types of food items although some difference existed, in proportion, according to size. After trout began preying on shiners, volume of shiners consumed, or degree of predation, was quite different for three size groups of trout. The present study describes the mechanisms of this predation:- where, when, how and to what extent various sizes of rainbow trout prey on redside shiners in Paul Lake.

DETAILS OF FIELD STUDY

In order to assess where, when, how and to what extent trout preyed on shiners the study was broken into several facets.

These were as follows:-

1. Factors affecting where and when predation took place. To answer these questions studies of the size and density distribution of both trout and shiners were carried out.

2. The actual activity of predation. This was studied by observing trout when preying on shiners. Also, since it appeared that small trout did not prey on small shiners, reasons for this were investigated by means of direct observations in the lake and trough experiments at the Institute of Fisheries, University of British Columbia. In the trough experiments four to six inch

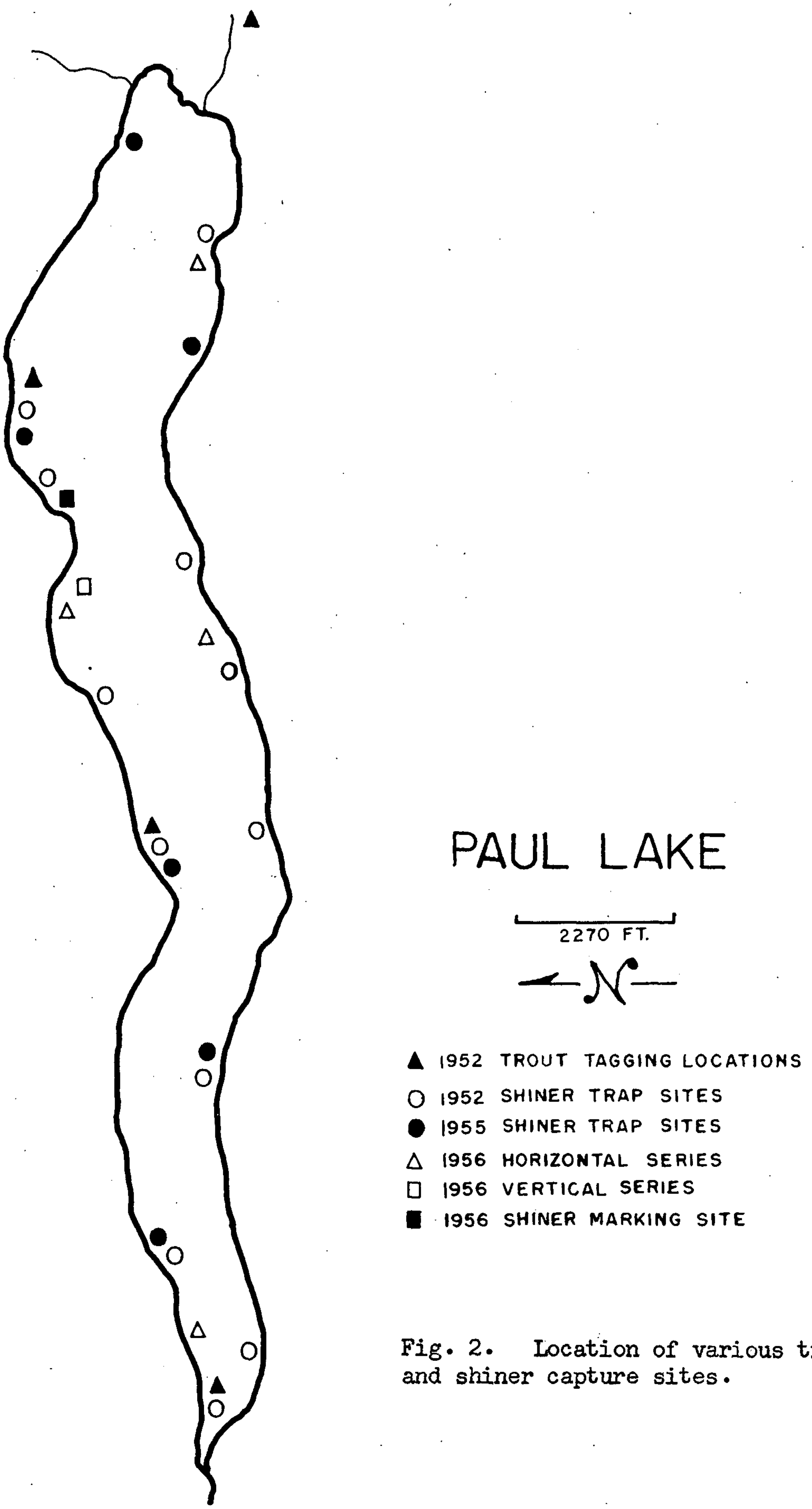


Fig. 2. Location of various trout and shiner capture sites.

trout were held with varying numbers of various sizes of shiners and observations made of the results of their feeding activities.

3. The extent to which various sizes of trout preyed on shiners. The size and number of shiners consumed was determined from stomach samples of 1603 trout taken in the summer of 1955 and 1956 and 86 in the winter of 1955-1956.

(1) Factors affecting time and place of predation.

(a) Distribution of trout in Paul Lake in summer.

From May to October 1952, outbound anglers were given a map of Paul Lake and 10 numbered tags. The map was divided into sections corresponding to areas designated on the lake by means of large signs and an imaginary line at lake-centre. Tags were placed on each trout as it was caught and the number marked in the approximate position on the map. Examination of catches upon the anglers' return enabled tabulation of number of trout, vital statistics and stomach contents of trout, with reference to location.

(b) Movements of marked trout.

Trout caught by means of trapnets and gillnets from May to September 1952, were marked with numbered, aluminum, maxillary tags and released. Trout in the spawning run in Upper Paul Creek were tagged at the egg-taking station during upstream migration. Marked trout were recorded from the trap and gillnet catches, anglers' catches and the downstream migration.

(c) Size and number distribution of shiners.

Data on the sizes of shiners and the number of shiners at various places about the lake throughout the season were obtained by several means. In May 1955, seven double conical wire mesh minnow traps were randomly placed around the shore of the lake before the time shiners were to be seen in this zone. These traps were suspended at mid-depth at the shore line. Traps were emptied every second day, the number of shiners and individual sizes recorded and the unbaited traps replaced empty. Direct observations were made of the size and number of shiners at various intervals from shore in fixed strips across the lake.

Attempts were made in 1952 and 1955 to determine vertical distribution of shiners by means of vertical series of minnow traps; gillnets also were used in 1955. Gillnets of one-half, three-quarters and one inch mesh were buoyed with additional floats in order to catch fish at known depths.

(d) Movements of Shiners

In 1952 shiners caught by means of minnow traps at various locations about the lake were marked with different fin clips and recoveries recorded for movement studies. Diurnal movements were recorded in 1955 and 1956 with the use of direct observations and small mesh gillnets. Horizontal seasonal movements across the shoal were recorded in 1956 as catches in series of minnow traps set across the shoal. Four series, of three traps each, were used. Each series consisted of a trap at the shoreline, one anchored at midshoal, one foot below the surface, and one anchored at the drop-off, one foot below the surface. Horizontal movements across the lake were followed by a marking and recovery programme in August 1956. Shiners were captured with a purse seine, fin clipped and released. Gillnets were set at intervals across the lake to see how far marked shiners moved.

Vertical movements of shiners over the shoal were recorded as catches in a single series of three traps. This series consisted of one trap on the bottom or shoal (10 to 12 ft. depth), one trap at mid-depth and one trap at the surface.

(2) Activity involved in predation.

Direct observations made, on the lake, incidental to work on other phases of the study, are presented as a description of what took place, characteristically, during predation. Many times the opportunity arose to observe at close hand large trout pursuing and catching shiners. These observations are included as the behaviour of adult trout when preying on shiners.

Some direct observations on small trout in contact with shiners were made and are briefly presented below. A number of simple, feeding experiments were carried out in the laboratory of the Institute of Fisheries. These were designed to test whether small trout (4-6 inches) could and would eat small shiners. The deterrent effect of large shiners, on the predation of small shiners by small trout, was also tested.

(3) Utilization of shiners by trout of various sizes in relation to other food items.

In order to evaluate the utilization of shiners as food, or the degree of predation, by various sizes of trout, weekly samples were taken from the anglers' catch. The trout were measured and a sample of scales taken from below the dorsal fin. The trout were eviscerated and the viscera removed for stomach analysis and sex determination. Viscera were preserved in 10 percent formalin and examined later.

Stomach contents were divided into five categories; shiners, plankton, bottom organisms, surface organisms, and miscellaneous. Plankton included all zooplankton forms except bottom dwelling amphipods. Bottom organisms included such forms as amphipods, leeches, gastropods and immature stages of various aquatic insects of orders Odonata, Diptera, Trichoptera and Ephemerida. Surface organisms included the adult forms of aquatic and terrestrial insects. Any unidentifiable material, plant material or remains of obvious bait were included in the miscellaneous category.

The contents of each stomach were separated into these various categories, the volume of each category determined by displacement of water and the total volume determined from the sum of category volumes. In addition to this, in 1955 the length of each shiner in the stomach of a trout was measured, and the volume determined. In each case in 1955 the number of shiners in the stomach was noted. Positive identification of fish remains, in the stomachs of trout, as those of <u>Richardsonius balteatus</u> and not of <u>Salmo gairdneri</u> was possible for two reasons. Shiners retained their body shape and characteristics up to 14 hours after being eaten by a trout. Shiners in Paul Lake are heavily parasitized by the intestinal cestode <u>Ligula intestinalis</u>. According to Bangham and Adams (1954) this cestode does not parasitize rainbow trout in Paul Lake. Almost invariably when identification was not possible from body shape and size, the presence of ligula in the remains made it obvious that these were the remains of redside shiners.

Samples were obtained in December 1955 and January 1956 with gillnets set under the ice on the shoals. These were used to compare summer and winter diet of trout.

Similarities in characteristics of the two species of fish have led to a competitive interaction. Common diet, and common dependence on the shoal as the area of greatest food production are two of these. Competition will not be dealt with but a general tabulation of some of the characteristics of predator and prey is useful as an introduction to the discussion of their interaction.

CHARACTERISTICS OF THE PREDATOR

<u>Size Distribution</u>:

Size distribution of trout as shown in Figure 3 is that of a sample of the anglers' catch from May to mid September. This sample is therefore an inaccurate estimate of the proportion of small trout in the lake. The legal

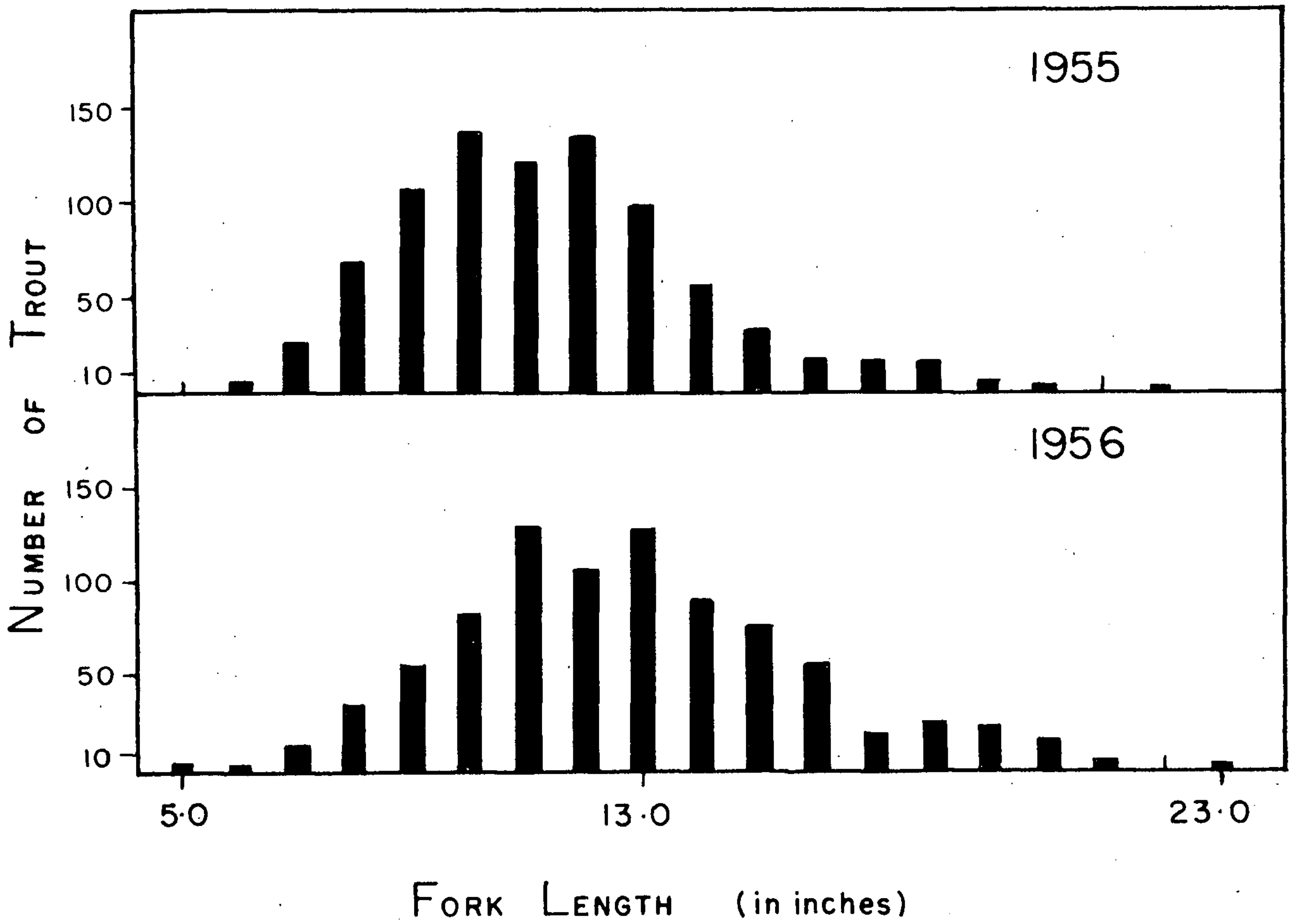


Fig. 3. Size distribution of a sample of trout from the anglers' catch, May to September 1955 and 1956.

Histograms represent size groups at one inch intervals.

size is six inches and not many of these are kept by anglers. However the size distribution beyond 10 inches is perhaps an approximate indication of the proportion of trout of these sizes in the population. Since trout under 10 inches in length do not prey on shiners this distribution can be used as an indication of the proportional representation of sizes of trout which do prey on shiners in Paul Lake.

The size range of the sample in 1955 was 6.75 inches to 22.0 inches. The mean was 11.6 inches. The range of the 1956 sample was 5.25 inches to 23.5 inches and the mean size was 13.1 inches.

Apparently maximum size of trout in Paul Lake has been nine and one-half pounds, recorded in 1931 (Mottley 1932). Larkin et al (1950) describe the decline in number of fish over four pounds, caught in Paul Lake, as indicating a declining growth rate from 1931 to 1936. This fluctuation in numbers of large fish taken closely follows the change in growth rate in the lake. The numbers of large trout taken was lowest in the years 1950 to 1954 but catches in 1955 and 1956 showed increases in numbers of four, five and six pound trout. The largest trout recorded in the 1955 and 1956 sample was 22 inches and six and one-half pounds. Female trout as large as 24 inches (four pounds plus) were recorded in the 1955 spawning migration.

Age Composition:

Table II gives a summary of the percentage age composition of the anglers' catch for various periods from 1936 to 1956. Changes in the contribution of year-old trout, as demonstrated by comparing the 1946-1949 figure with that of 1952, are partly the result of the drastic reduction in growth rate after the entrance of shiners into the lake. The very low figure for one-year-old trout in 1955-1956 is an artifact of the yearling liberation policy. Whereas from 1936 to 1949 yearling and two-year-old trout made up the bulk of the catch, it

TABLE II

Percentage Age Composition of the Anglers' Catch from Paul Lake for three periods from 1936 - 1956.

<table>
<tr><th rowspan="2">Year</th><th colspan="5">Age</th></tr>
<tr><th>I</th><th>II</th><th>III</th><th>IV</th><th>V</th></tr>
<tr><td>* 1936-1937</td><td>25.9</td><td>39.8</td><td>24.2</td><td>9.1</td><td>1.0</td></tr>
<tr><td>* 1946-1949</td><td>34.0</td><td>34.4</td><td>26.0</td><td>5.3</td><td>0.3</td></tr>
<tr><td>✓ 1952</td><td>1.3</td><td>18.4</td><td>60.4</td><td colspan="2">19.9</td></tr>
<tr><td>1955-1956</td><td>6.1</td><td>68.9</td><td>20.5</td><td colspan="2">4.5</td></tr>
</table>

* From Larkin et al (1950)

✓ From Larkin and Smith (1954)

TABLE III

Percentage Age Composition of Three Size Groups in the Anglers' Catch of Trout in Paul Lake in 1955-1956.

<table>
<tr><th rowspan="3">Size Groups F.L. in Inches</th><th colspan="8">Age</th></tr>
<tr><th colspan="2">I</th><th colspan="2">II</th><th colspan="2">III</th><th colspan="2">IV</th></tr>
<tr><th>No.</th><th>%</th><th>No.</th><th>%</th><th>No.</th><th>%</th><th>No.</th><th>%</th></tr>
<tr><td>6 - 10</td><td>12</td><td>20.0</td><td>46</td><td>76.6</td><td>2</td><td>3.4</td><td>--</td><td>--</td></tr>
<tr><td>10 - 14</td><td>2</td><td>1.7</td><td>88</td><td>72.7</td><td>25</td><td>20.7</td><td>6</td><td>4.9</td></tr>
<tr><td>14 - 14+</td><td>1</td><td>1.7</td><td>34</td><td>53.9</td><td>23</td><td>36.5</td><td>5</td><td>7.9</td></tr>
</table>

is now two and three-year-old trout which constitute the major part.

While five-year-old fish constituted never more than one percent, the absence of this age in the 1955 and 1956 catches is no doubt partly the result of the stocking programme and the rigorous selection of the fishery. The fishery selects faster growing fish first (Larkin and Smith 1954) but is perhaps also intensive enough to harvest the fish before they reach five years of age. The fact that the fishery is probably dependent on the yearling liberations, which will not contribute five-year-old trout until at least 1958, is also partly responsible for the absence of five-year-old trout in Paul Lake.

Table III indicates the age composition of the three size groups into which trout will be divided in this study.

Growth rate is variable, and the population consists of some natural production in addition to the liberated yearlings. As a result of this, one-year-old trout range in size from six inches to at least thirteen inches or more. Liberated yearlings enter the fishery, as I + fish, in mid August of the year they are liberated. They are, at this time, an average of 8.4 inches fork length. By early May of the following year these liberated trout, as II + fish, have attained a mean length of 11.5 inches.

It appears then that trout in Paul Lake, at least those liberated, reach a size of 12 inches by their third summer as II + fish. Maximum size is probably between 20 and 30 inches and maximum age four or perhaps five years. No more than 10 percent of the anglers' catch is made up of the four and five-year-old trout and the largest percentage of the large trout taken are two years of age.

Sex Ratio:

The anglers' catch of trout from Paul Lake has always shown a predominance of females. The sex ratio for whole seasons in years 1946-1949 and 1955-1956 are shown in Table IV.

TABLE IV

Sex Ratio of Trout from Anglers' Sample 1946 - 1956

Year	Males		Females	
	No.	%	No.	%
1946-1949	227	41.0	339	59.0
1955	331	42.3	451	57.7
1956	288	38.8	454	61.2

Larkin et al (1950) state that this disproportion between the sexes is probably the result of a greater life expectancy in females than in males. Males commonly spawn at age two and the disproportion between sexes is marked from age two onward. The catch of yearling marked trout in the fall of 1955 showed a 1:1 sex ratio.

Maturity:

As stated above some male rainbow trout spawn at age two and some spawn more than once. From August 29th to September 18th 1956, 97 trout 8-10 inches in length were taken by gillnet in the area of the outflow of Upper Paul Creek. Sixty-five percent of these fish were maturing males showing a high degree of gonad development. Female rainbow trout in Paul Lake generally spawn for the first time in the third or fourth year of life. These trout do not spawn each year and only a small proportion survive to spawn a second time.

Spawning Migration:

Mottley (1933) gave the following description of the spawning migration in Paul Lake. The spawning run is coincident with the first warm spell of weather in May. At this time large numbers of trout enter Upper Paul Creek each afternoon. The primary factor involved is volume of outflow, and temperature is secondary. The peak of the run comes when the density of the creek outflow is such that the water enters the lake at the optimum level for adult trout, (temp. of 6-10°C.). Since males are more active than females at this time they find this stream sooner and in the first 12-14 days of the run males exceed females. The peak of the run lasts approximately 14 days and toward the end females far exceed males. After the peak, the run consists of female stragglers for approximately a week and then ends. The end is perhaps partially due to a depletion of adult fish or to the disruption of the attractive force of the outflow. This disruption is perhaps the result of warm outflow spreading out closer to the surface of the lake.

Survivors of the spawning run have usually returned to the lake by mid-June.

CHARACTERISTICS OF THE PREY

Size Distribution:

Fig. (4) shows the size distribution of shiners in the catches of seven minnow traps fishing around the perimeter of the lake from June 8 to September 15, 1955. The fluctuations in numbers of various sizes of shiners is possibly the result of the onshoal-offshoal movements to be described below. The steady rise in the number of 1-1½ inch shiners represents the entrance into the catch of the fish of the year. The seasonal mode, represented by 2½-3½ inch shiners, is the size of shiners seen in extreme concentrations on the shoals in late June and early July. The largest shiners seen in the lake were 4½ to 5 inches (F.L.). This seemed to be maximum size for this species in Paul Lake. Lindsey (1950a) gives the estimated mean standard length of shiners in Pinantan Lake (above Paul in the lake system) as 1.1 inches at year 0, 2.2 inches at year I and 2.9 inches at year II. These sizes are stated as at September 1st. The writer also notes the difficulty in aging shiners by size frequency as a result of the difference in the rate of growth of the

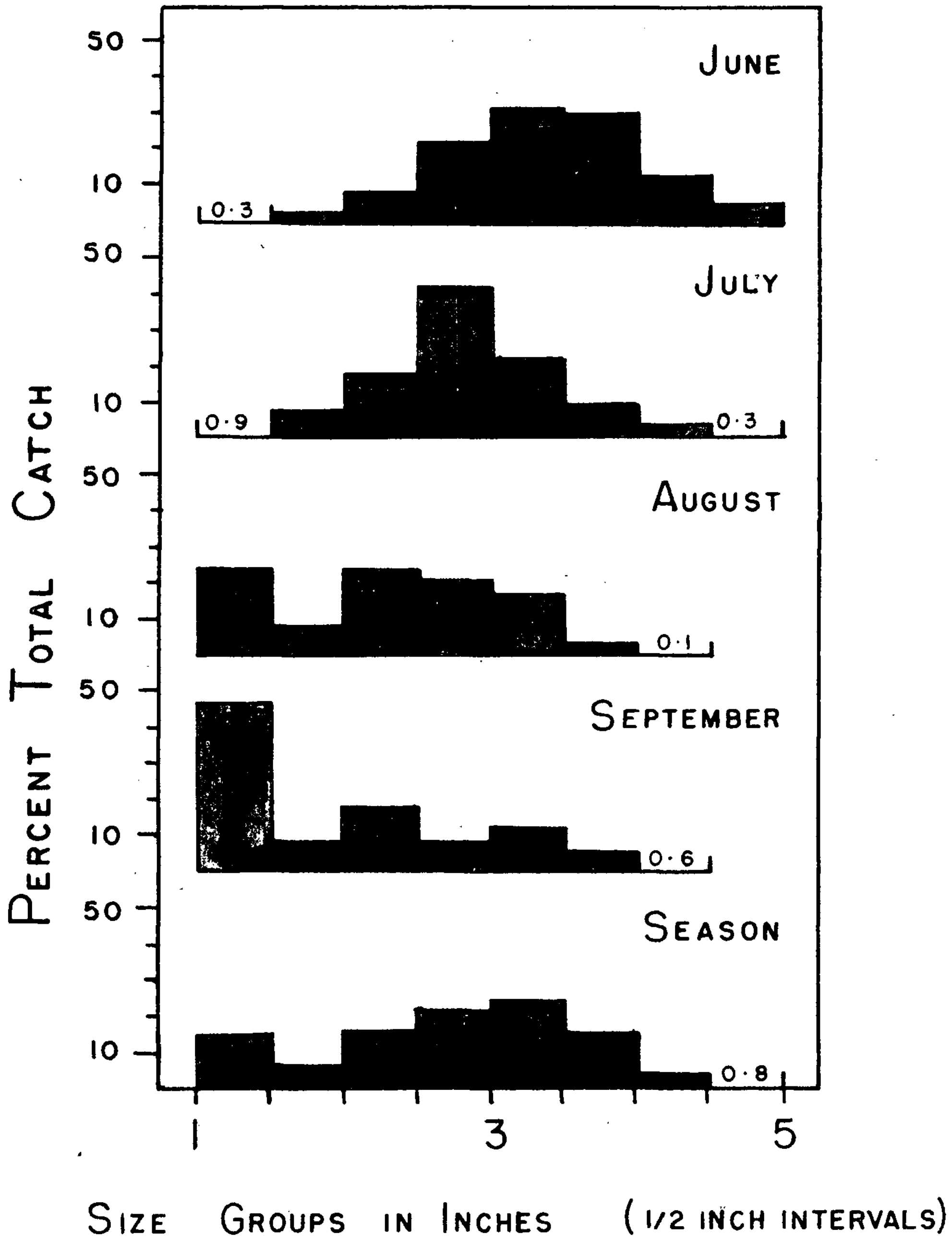


Fig. 4. Size distribution of shiners by month and season 1955.

sexes. However the size frequencies given in Figure 4 correspond roughly to those given by Lindsey so that one might deduce an approximate growth rate.

Estimated fork length range in inches, for shiners in Paul Lake on September 1, 1955.

Year 0	Year I+	Year II+
$1-1\frac{1}{2}$	$1\frac{1}{2}-3$	3-4

Those included in year 0 are shiners hatched during the summer (perhaps as early as June 28th) and having attained this size by September 1. Those included in I+ are those hatched the previous year. Numbers taken for sizes over four inches are too small to make any estimate but it seems likely, from this growth rate, that maximum age is III+ or IV+ at the $4\frac{1}{2}$-5 inch maximum size range.

Sex Ratio:

From samples taken in 1955 and from Lindsey (1950a) it appears the sex ratio of redside shiners does not differ significantly from a 1:1 ratio ($P=0.8$). In five samples totalling 178 shiners there were 87 females and 91 males.

Spawning:

It appears shiners spawn to a greater extent in Paul Lake itself than in the creeks. Small shiners appear all around the shore in greater numbers than are ever seen in the creek or at the creek mouth. Choice of spawning grounds is not rigid as fry appear in areas of exposed sand and dense vegetation. The spawning period is protracted since individuals spawn at different times and may spawn more than once.

In 1955 ripe males and females were first taken in minnow traps on June 10. The peak of ripe individuals was about June 16. The last ripe female was seen toward the end of July and males in the first week in August. Free swimming shiner fry appeared in the first week of July. Lindsey (1950a) estimates that the spawning period of shiners in Rosebud Lake, British Columbia, extends from the last week in May to the first week in August. On May 15, 1956, ripe males were taken in deep water before they appeared on the shoals. Many males were at this time showing signs of sexual maturity.

Eggs are laid between dusk and dawn, they are adhesive and are broadcast. These eggs adhere to the substrate or vegetation and hatch in approximately eight days (Lindsey 1950a).

FACTORS AFFECTING TIME AND PLACE OF PREDATION

Primary in any consideration of the predation of rainbow trout on redside shiners are those factors which bring the two together or isolate them. The distribution and movements of the two species during the season greatly influence the degree of predation.

A. Distribution of rainbow trout in Paul Lake

Figure 5 shows the areas into which the lake was divided for the purpose of plotting the distribution of the anglers' catch in May to September 1952. From this plotted anglers' catch it is possible to create a partial picture of the distribution of rainbow trout in Paul Lake over the summer. Figures 6a and 6c show the number of trout plotted in two ways. Figure 6a indicates the catch in each month as percent monthly total in each section. It is apparent from this figure that sections DE and FG dominate the monthly catches in the months of May, June, August and September. In July more trout were caught in section BC. This figure reflects, to a certain extent, the tendency of anglers to fish in that area which is the shortest distance from the cottages. Summer cottages are concentrated on the south shore of section FG.

When the data in the histograms in figure 6a are combined in two seasonal

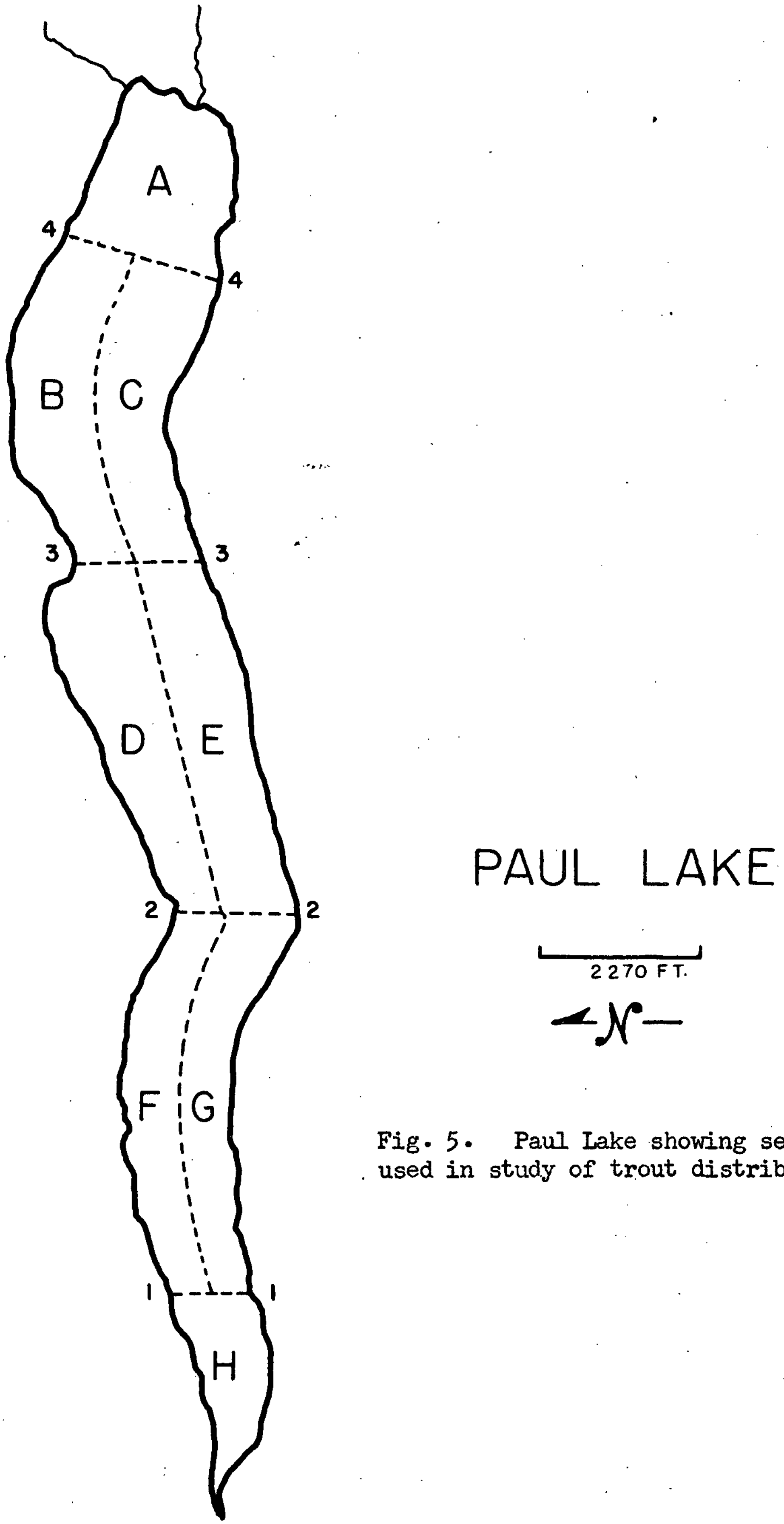


Fig. 5. Paul Lake showing sections used in study of trout distribution.

periods, May and June, and July and August and September, it is possible to show net gain or loss in numbers of trout in each section over the summer. Section A drops from 11 percent in May-June to eight percent in July-September. This is a net loss. Sections FG and H show similar net losses when combined in this fashion. Loss in Section H is small, approximately 1 percent. The areas which show a net gain are BC, (increasing from 14 percent to 22 percent) and DE (increasing from 28 to 37 percent). In order for sections BC and DE to show a net increase when the other sections decreased trout must have moved out of areas A, FG and H and into areas BC and DE in the period from July to September.

Figure 6c graphically presents the catch in each section, as percent total monthly catch. The sections are arranged as on the map of the lake. From the curves in this figure there is an indication that when catches are down in other areas in July they go up in BC and DE. This also emphasizes a movement into these areas.

Figure 6b represents the catch of two size ranges of trout in the sections of the lake for the same two time periods discussed above. The catches are expressed as percent seasonal total catch in each section. It can be seen that in section A there is a decrease over the season in large trout, so that the net loss expressed above must be large fish (13-18 inches) moving out. This is also the situation in section FG, out of which both small (8-12 inches) and large trout seem to be moving. While there was a very small net loss in H the size change is such that any loss was large trout. Some small trout may have moved in. Sections BC and DE showed net gains. These gains constitute fish moving in. Possibly it is a movement in of both large and small trout.

The gradual change, from section A to section H, in slope of the size lines, indicates that, considering the lake as a whole, the west end contains more large fish than the east end. Movement of large trout into sections BC

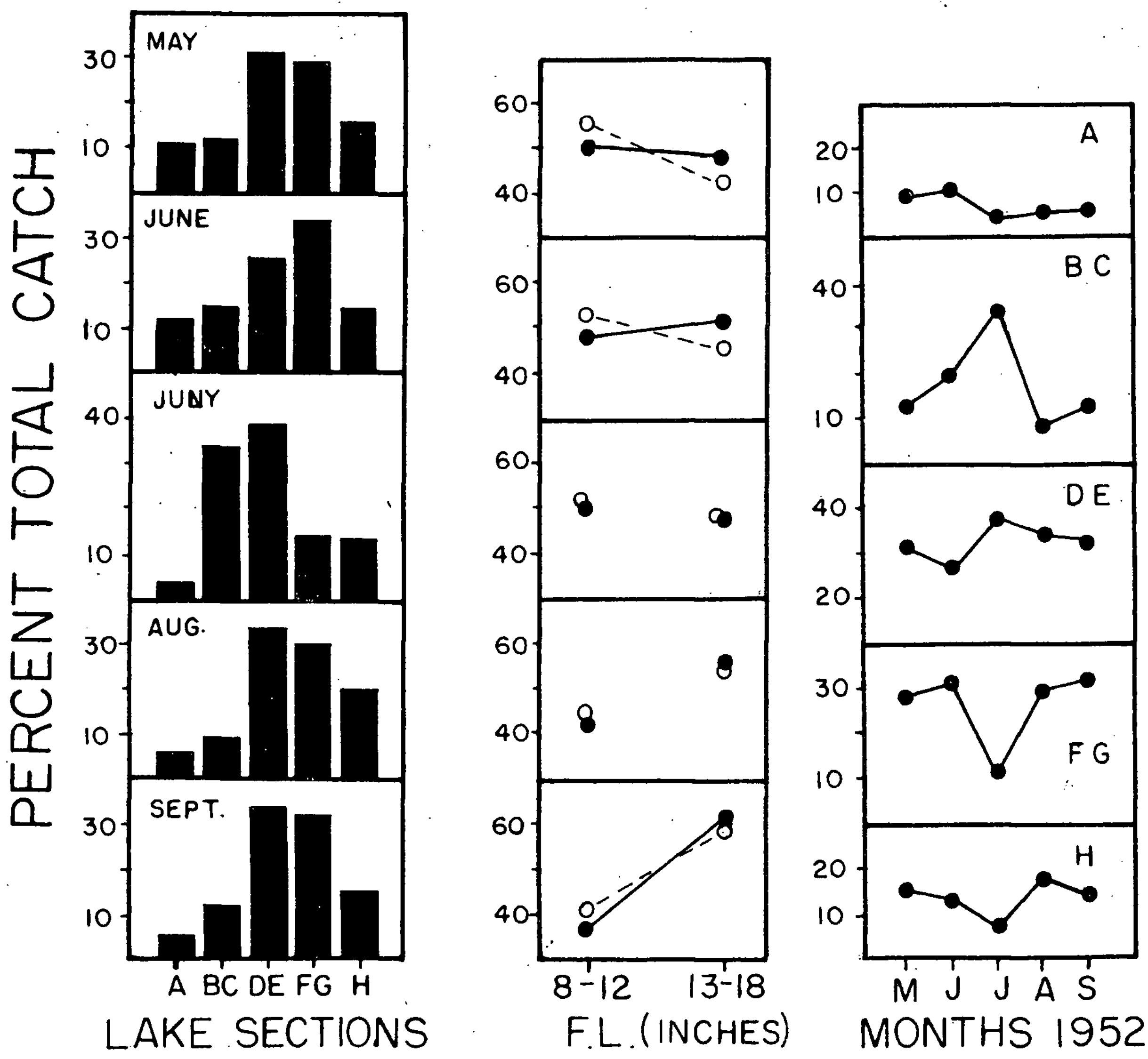


Fig. 6a. Fig. 6b. Fig. 6c.

Fig. 6a. Anglers' catch of trout by sections as percent total monthly catch.

Fig. 6b. Catch of two size ranges of trout, in two time periods as percent season total. Closed circles May and June - open circles July, August and September.

Fig. 6c. Percent total monthly catch of trout by sections.

and DE might easily be from the western sections of the lake.

This work in 1952 indicates that trout move out of sections A, FG and H in the period of July to September. In this period there is a movement into sections BC and DE. Analysis of the size of trout being caught in these two time periods indicates that it is large trout, in the size range, which prey on shiners, which appear to be moving into these sections.

B. Movements as Indicated by Recaptures of Marked Trout

In 1952, 1155 trout were tagged between May 16 and September 23. The tagging sites are shown in Figure 7. Trout migrating upstream were tagged at the egg collecting station (Site 1). Tagging site 2 consisted of a trap net fishing between May 16 and September 19. Site 3 consisted of a trap net set from June 5 to September 24. Site 4 was a trap net operated from June 20 until September 25. Site 5, a Wolfe trap on Upper Paul Creek, was operated between August 18 and September 23.

Recaptures of marked fish were made at these same sites as well as in various gillnet catches and in the anglers' catch. Recaptures were recorded in 1953 and 1954 at the egg collecting station (Site 1). Table V gives a summary of trout tagged and recaptured. Table VI shows the number of trout tagged and recaptured at various sites and by other means. The totals in Table VI do not agree with the total given in Table V as some of the recapture records have no exact position data. Others that were marked at Paul Creek egg taking station during upstream migration, were recaptured at this point during the downstream migration and recaptured later elsewhere. These are recorded as recaptures at the final position. Those recorded as having been tagged at Site I and recaptured at this site are those which were recaptured there and never seen again. Table VII shows the number of trout from each tagging site recaptured by anglers in various areas of the lake. Figure 7 shows the approximate position of these recaptures in the sections.

TABLE V

Number of trout tagged and recaptured.

Number of trout tagged - 1952	1155		
Number of trout recaptured - 1952		132	(all sources)
Number of trout recaptured - 1953		57	(Paul Cr. Trap)
Number of trout recaptured - 1954		12	(Paul Cr. Trap)
Totals	1155	201	

TABLE VI

Number of trout tagged and recaptured by various means in 1952-1954.

Tagging Site	No. Tagged	Site of Recapture							
		1.	2.	3.	4.	5.	G.N.S.	Anglers	Total
1.	448	49	0	1	0	0	0	11	61
2.	69	2	1	1	0	0	1	7	12
3.	476	41	0	8	0	2	2	28	81
4.	161	15	0	0	1	0	0	12	28
G.N.S.	1	0	0	0	0	0	0	0	0
Totals	1155	107	1	10	1	2	3	58	182

Recaptures at Site 1 (except) were in 1953 and 1954 spawning runs since most fish were marked after 1952 run.

Recaptures in 1952.

Gillnet sets.

The small number of tags of Site 1 origin (Paul Creek Trap) recaptured later in the lake is perhaps the combined effect of tagging and spawning mortality. In 1952, 448 trout were tagged during upstream migration, 49 of these were recaptured during downstream migration and only 12 of them recaptured by other means in the remainder of 1952. There were no tags of Site 1 origin in the spawning migrations of 1953 and 1954. As opposed to this, of 476 trout tagged as "clean" fish at Site 3, 27 were taken by anglers in 1952 and a total of 41 were taken in the spawning runs of 1953 and 1954. Three of these trout were captured in both the 1953 and 1954 migrations. Of 161 trout tagged at Site 4, 13 were recaptured in 1952 and 15 were taken in the spawning migrations of 1953 and 1954.

Fish marked while weak from migration no doubt suffered higher mortality than fish in good condition marked at the other sites.

At Sites 3 and 4, trout too small to be tagged were marked by clipping the adipose fin. There were no reports of the capture of clipped fish in 1952 or 1953.

The recaptures of tagged trout in Paul Lake appear to be widely distributed. Of those fish marked at the east end of the lake as many were recaptured in the west end as in the east end. While more tags of central origin were caught close to the tagging site than elsewhere, this may only reflect the high angling intensity here as well as a greater number of these tags in the lake. Of the total of 1155 trout tagged, 41 percent were tagged at Site 3. Trout tagged in the central position of the lake did move in both directions from this location. At least some trout from the west end of the lake moved the entire length of the lake in order to spawn in the inlet stream. Access to the outlet stream is blocked by a dam. Of those trout tagged migrating upstream that survived to re-enter the lake, 12 were caught. Five of these were taken in the west half of the lake.

One can infer, however, that at least in 1952 there were no discrete

TABLE VII

Recaptures, by anglers, of Tagged Trout in Each Area of the Lake.

Area of Capture	Tag Origin				Totals
	Site 1	Site 2	Site 3	Site 4	
A	1	0	0	0	1
BC	0	1	3	2	6
DE	6	3	10	4	23
FG	3	2	14	2	21
H	1	1	1	4	7
Total	11	7	28	12	58

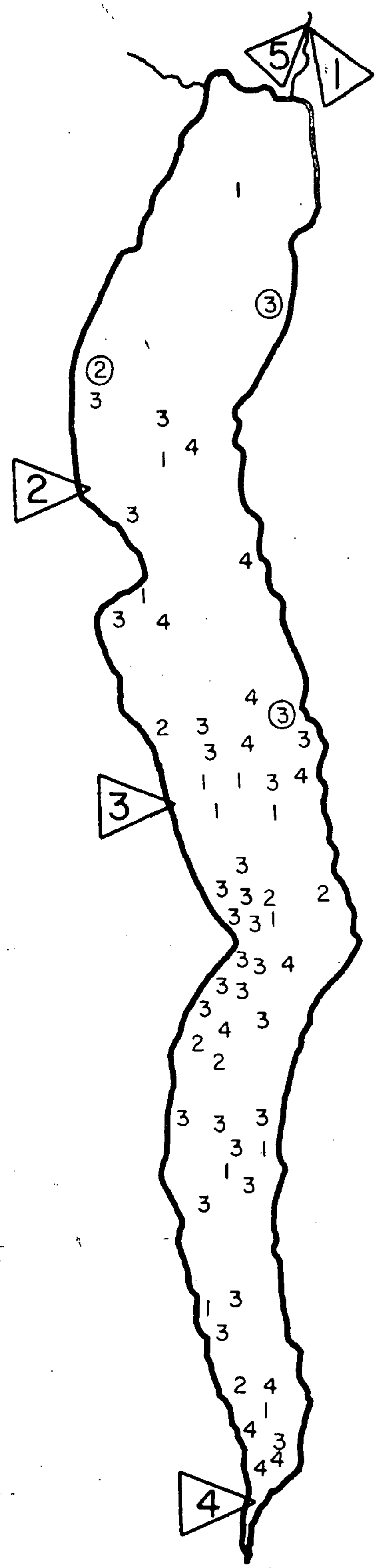


Fig. 7. Tagging sites and recaptures of tagged trout according to tagging site.

Numerals in lake enclosed by circles indicate recaptures in gillnets, others by anglers.

populations of trout at any one place at any one time. The trout seemed to move about freely from place to place over the length of the lake, at times moving from one end of the lake to the other. This tendency makes possible the distribution pattern by sections, in the two time periods, as described above. The free movement of tagged trout lends strength to the possibility that large trout move into sections BC and DE in the period July to September.

C. Size and Number Distribution of Shiners

(i) Distribution around Perimeter of Lake.

Data on the distribution of shiners in the summer months is derived from three sources. Size, number and spatial distribution are indicated by the daily catches of seven, conical, wire minnow traps. These were randomly placed around the shoreline of the lake at a time when shiners had not, as yet, appeared. Crude estimates of distribution were gained from day to day observations of the shiners. Crude quantitative estimates were made on the basis of weekly strip counts. These consisted of rowing from shore to shore between each of the sets of numbered markers on the lake and noting the number and approximate size of shiners at various distances from each shore. Further information on the spatial distribution of shiners was gained from the catches of small mesh gillnets. Figure 8 shows the daily total catch of shiners in the minnow traps.

On May 6, 1955, an exploratory examination of the lake showed that shiners were in evidence only in the outlet bay at the west end of the lake. There were approximately 30-50 shiners, two inches to four inches in length, around and in the screened irrigation outlet.

Shiners were first seen in the lake on May 28 when approximately 20 were observed under a boat dock on the south shore. There were no shiners visible around the shore when the shiner traps were set out on May 28. Nor were

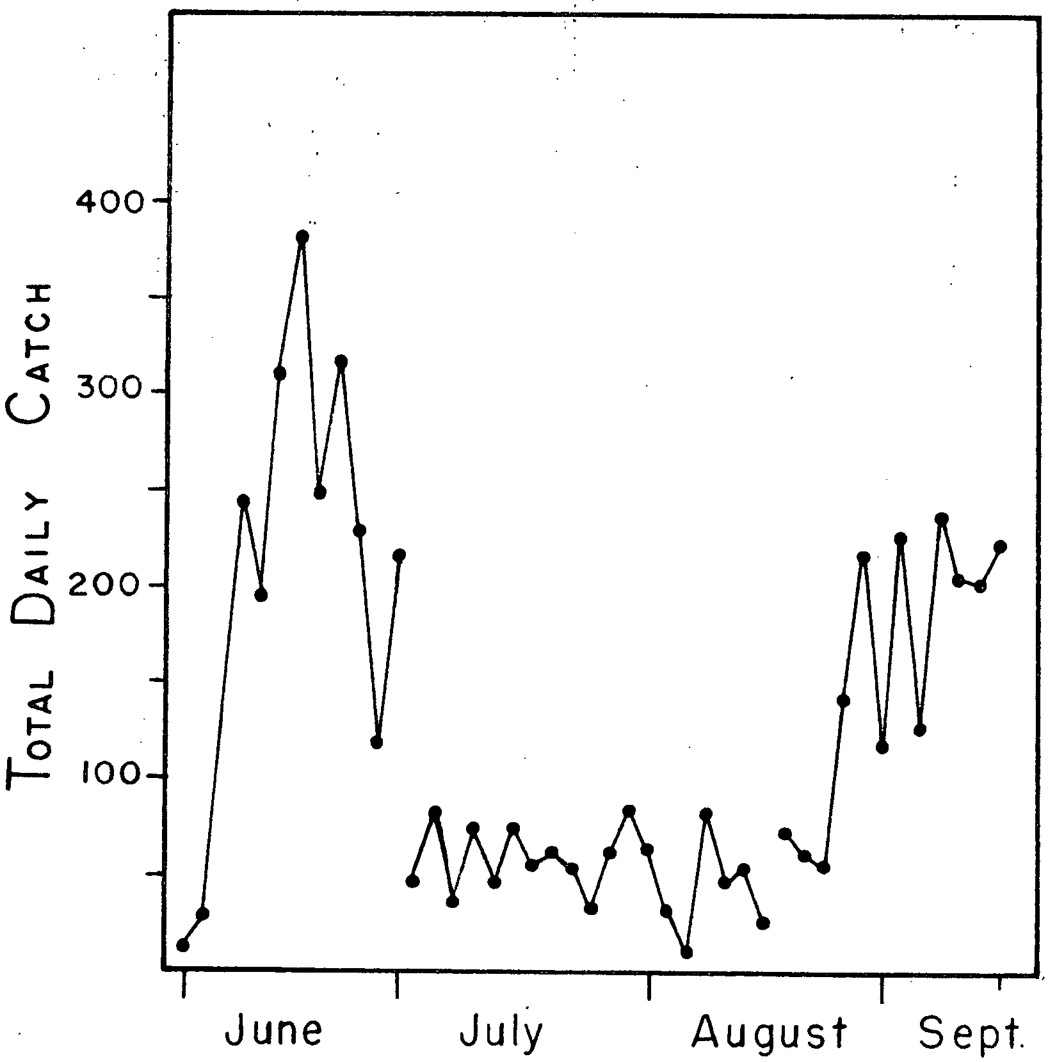


Fig. 8. Total daily catch of shiners June 2 to September 15, 1955.

Totals are those for 7 minnow traps emptied every other day.

there any visible anywhere in the day time, when a gillnet was set near Agnes Creek, on that day. Although there were no shiners present along the shore line during the day, when the gillnet was lifted on May 30 the net had caught 500-600 shiners in the two days it had been set. The percentage size distribution of a sample of 200 of these showed the shiners to be:-

$3-3\frac{1}{2}$ inches	9.5%
$3\frac{1}{2}-4$ inches	71.5%
$4-4\frac{1}{2}$ inches	20.0%

This same day one shiner was seen near a shiner trap (south shore, east of Gibraltar rock, see Figure 2) and shiners first appeared in the shiner traps.

In the first week of June a school of over 100 shiners of all sizes was seen at marker No. 4 north (see Figure 5). The shiners were in amongst the floating sticks and brush along the shoreline. The shiners exhibited a vertical stratification of sizes with the smallest shiners close to the surface and the largest (4-5 inches) closest to the bottom. This group of shiners was swimming in the top 1-2 feet of water in a total depth of four to five feet. Smaller schools appeared at a point one-third of the way between markers 3 and 4 north, and at marker No. 1 north. These also were near the surface and in close association with brush or broken brances floating in the water. The surface temperature at this time was 56°F.

By the middle of June large schools consisting of shiners of all sizes, showing vertical stratification, developed at many points along the north shore. They had started to move out from the shore to the full extent of the shoal (shoal ends a maximum of 150 feet from shore) remaining in the top 1-3 feet of the total depth of 12-15 feet of water.

While daytime observations indicated a relatively greater abundance along the north shore as compared to the south shore, the plotted catches for north and south shore traps (Figure 9b) indicate that the catches, at this time, were greater in the south shore traps. However in the months of July, August and September catches on the north shore exceeded those of the south shore.

In the last week of June the larger shiners seemed to be found predominantly 25-50 feet offshore. Only the smaller sizes seemed to be remaining close to shore. Wherever possible the shiners were still oriented around fallen trees or shrubs, floating or submerged in the water. When undisturbed the shiners would remain still with their heads toward the branches of the tree or shrub. The school, oriented in this way, would completely surround the brush. Shiners were apparent in an almost unbroken line along the north shore from marker No. 1 to marker No. 4. Daytime observations placed the number along the north shore as twice that along the south shore.

In the first week of July (July 4, 1955) newly hatched shiner fry began to appear and within a week there were large numbers to be seen close to shore all around the lake. At this time there appeared to be horizontal size stratification (similar to that described by Lindsey 1950, in Rosebud Lake, B.C.) as well as vertical.

In mid July the shiner fry also began to move offshore so that the number of shiners close to shore was greatly reduced. By mid July, on the shoal at Swampy Point (100-200 feet offshore), there had formed an aggregate of shiners numbering in the thousands. There was no other large group between this point and no. 4 marker north. Toward the end of July the shiner fry seemed to be joining the bigger fish offshore. For a period of about one and one-half weeks at this time the shiners appeared to be swimming closer to the bottom than previously so that they were not as apparent around the shores as they had been.

By the end of the first week in August the shiner fry had grown to three-quarters of an inch in length and could be seen in discrete groups of 300 or so at intervals all around the lake. They seemed to be present in isolated schools at approximate intervals of 50-100 yards. Also their numbers seemed to be greater on the south shore than on the north in contrast to the larger shiners. Very often there would be two or three shiners three and one-half to four inches in length in the midst of the large school of smaller shiners.

In late August the aggregates of large shiners were still present at various places along both shores. More large shiners were observed closer to shore at this time than they had been previously. It seemed as if the schools of shiners were moving back toward shore. This is reflected in the trap catches. Also the fry had reached a size such that they were taken in the shiner traps, and the day to day catch figures show the prominance of this size in the catch from this point on. Toward the end of August the shiners appeared to be more evenly distributed over the shoal area from the shore to the dropoff. However, the larger shiners seemed to be isolated in large groups offshore and these fish assumed a small proportion of the catch in contrast to the spring when three to four inch shiners made up the largest part of the trap and net catches.

In early September the more even distribution prevailed so that the shorelines were not so devoid of shiners. The schools of large shiners were still in evidence on September 17 but the numbers in the schools were decreasing, and the larger fish disappearing from the shores. Reports from the lodge operator, subsequent to the termination of field studies, indicated that the larger shiners disappeared first and that very few shiners were to be seen in late October. Those few seen around the shore were of the smaller sizes. By freeze up in late November the lodge operator reported that there were no shiners seen anywhere around the lake, at least near shore.

In mid and late August one of the largest aggregates of shiners, consisting mainly of two to three inch shiners, was observed by the author in the bay on the east side of Swampy Point. This aggregation apparently was the result of having placed in the water at this spot a large wooden anchored structure to hold trout and shiners for observations. Although there had been a heavy concentration offshore and to the west of this point, two days after the structure was anchored there, hundreds of shiners accumulated at it, and oriented to it, as they did to the brush in the spring. This soon became one of the major areas for the predation of trout on shiners. It was here that most of the closer observations of the feeding of trout were made and here that trout were readily angled with dead shiners.

Throughout the summer shiners were attracted to anything different or any disturbance in the water. Whenever the boat passed through a school the fish would follow it; however they would follow the boat no farther than 15-25 feet beyond the dropoff. They would then turn about and swim back to the shoal.

Catches in the seven, lake perimeter, minnow traps as shown in Figure 8 indicate peaks in the total number of shiners caught in June and September. In the periods of July and August the catches were considerably lower. Analysis of the monthly catches of shiners in the various sections of the lake indicates that in June and July the greater numbers of shiners were taken in sections A and FG. (See Figure 9a). In August, however, catches in section BC rise to ne arly equal those in FG. In September the catch in section BC is over 50 percent of the total and far exceeds any other section.

Shiners in the three smallest size groups (1-$2\frac{1}{2}$ inches) seemed to remain together and isolated at times from those of larger size ($2\frac{1}{2}$-5 inches) as described above. Shiners in the larger group were those utilized by trout to the greatest extent, and the smaller shiners far less. The relative numbers of the two size groups as percent total monthly catch are plotted in Figure 9c. The catches of smaller shiners increased through the summer and the catches of large shiners decreased over the period.

(ii) Vertical distribution

Gillnets ($\frac{1}{2}$ inch, $\frac{3}{4}$ inch and 1 inch mesh) were set at various depths to discover the vertical distribution of shiners in Paul Lake. Nets were fished at various depths from surface to bottom at various times during the summer. As early as May 28th, when no shiners were visible about the shore, a gillnet

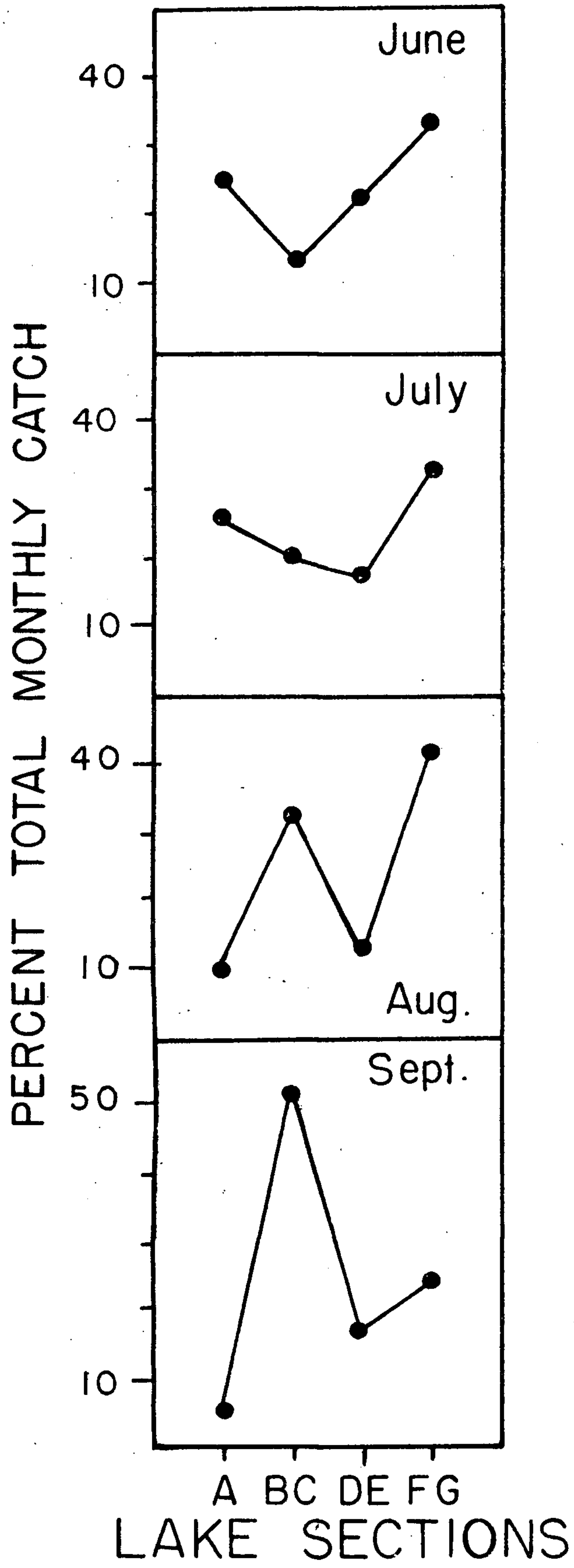


Fig. 9a. Percent total monthly catch of shiners in each section.

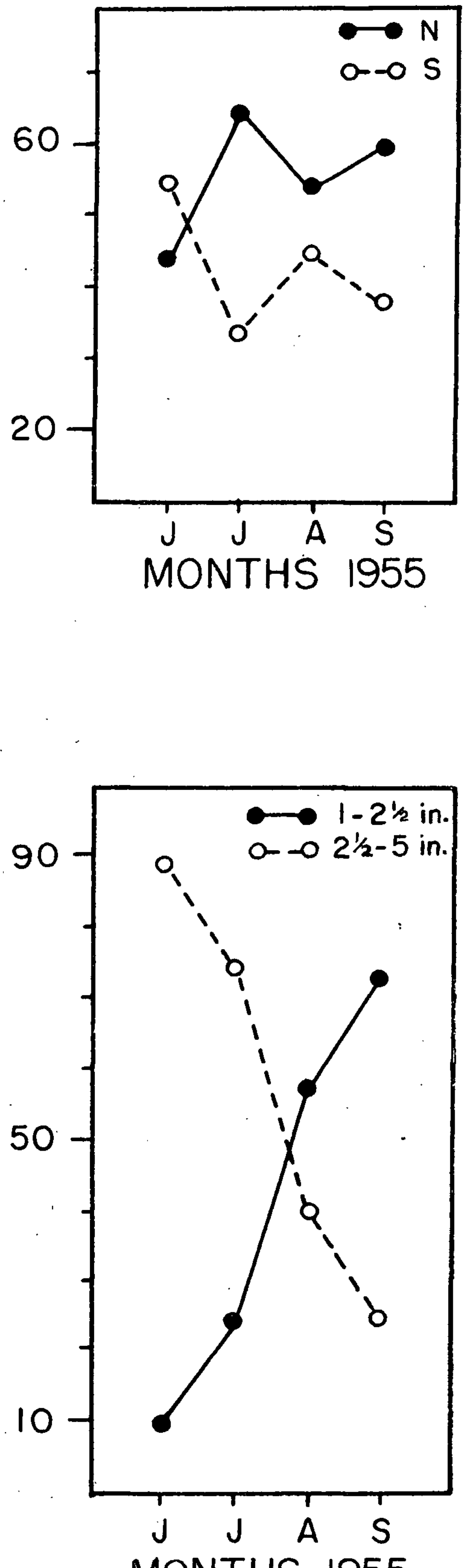


Fig. 9c. Catch of two size groups of shiners as percent total monthly catch.

set perpendicular to shore caught 500-600 shiners in a two night set. The net was set from shore to 50 yards offshore and was fishing from 1-30 feet of water. The shiners taken were all in the three inch to four inch size range and were all in the section of net fishing from 20-30 feet of water. Shiners were caught in the full width of the net in this section. There were no shiners in the section of net on the shoal. A gillnet set the following day 50 feet from shore in 12-20 feet of water showed no difference in the number of shiners on the offshore side (moving shoreward?) and those on the inshore side of the net (moving offshore?). There were no shiners in that section of the net in the turbulence of Agnes Creek (an intermittent inlet stream) so it appeared they were not moving into the creek.

Nets set perpendicular to the shore in June and July showed considerably fewer larger shiners in the 30-35 foot zone (catches of 50-75 in a one night set of 1 inch mesh net). In August and September when few large shiners were to be seen on the shoals similar gillnets sets again took large numbers of shiners. These catches correspond to the period of decreasing perimeter catches of shiners of this size (see Figure 9c).

During the summer, whenever shiners were present on the shoal, there existed a definite vertical stratification of sizes. The size increased with depth, that is, smaller shiners were found closer to the surface.

In 1952 vertical series of minnow traps set at intervals of 5 meters from surface to bottom took no shiners, so it was assumed that shiners were restricted to the shoals and shoal edge. In 1955 work to be discussed below showed that shiners could be taken in overnight gillnet sets in deep water. Gillnets buoyed to catch fish at various depths were set at lake centre and catches at various depths recorded. Over the whole summer period these overnight net sets took catches per night, as follows:-

Surface to 8 feet	100 - 1000
8 to 16 feet	100 - 300

17 to 24 feet	10 - 20
25 to 150 feet	0

Similar nets set during daylight took no shiners and careful observations at two hour intervals revealed no shiners present at lake-centre netting sites over the entire length of the lake. These catches contained all sizes of shiners and size distribution in the nets indicated that vertical size distribution appeared to be maintained on these locations also.

D. Movements of Shiners

(i) Horizontal movement around perimeter of lake.

In 1952 shiners were captured in nine minnow traps, and in three trapnets set for trout marking and recovery work. These traps were situated around the lake (open circles and closed triangles of Fig. 2). The total catch of shiners, including those dead when the traps were emptied, was 9,168. Of these, 5,343 were marked with various fin-clip combinations to designate area of capture. Of the 5,343 marked 203 were subsequently recaptured in various areas over the summer. Table VIII summarizes the marking and recovery. Figure 10 shows the marking sites and areas within which all shiners caught were given the same mark.

The greatest number of recaptures in any area were of the mark put on in that area. The three sites at the east end of the lake caught only shiners marked in that area. Site 5, on the north shore, caught marked shiners from the two adjacent areas of the north shore but none from the south shore stations. Site 6 in the same area, in addition to marks of its own area, caught shiners only from the area closest to it. Site 8 in the west end captured four shiners that had been marked at the east end of the lake, 10 shiners marked at central north shore sites, and only one shiner that had been marked on the south shore at Site 12. The data indicate localized populations in that the largest number of recaptures were of marks put on in that area. Some shiners, however, moved downstream almost the entire length of the lake and others moved at least half

TABLE VIII

Number of shiners caught, marked and recaptured at each site 1952.

Marking Site	Mark	Total Catch	Number Marked	Number of recap's from each marking zone *				
				L.V.	R.V.	D.	B.V.	D.+L.V.
1	Left Ventral	467	244	3	0	0	0	0
2		279	226	2	0	0	0	0
3		1135	352	1	0	0	0	0
4	Right Ventral	230	195	0	0	0	0	0
5		3030	1563	3	18	4	0	0
6		327	248	0	2	2	0	0
7	Dorsal	470	261	0	0	7	0	0
8		1987	1233	4	10	135	0	1
9		258	221	0	1	2	0	0
10	Both Ventrals	332	277	0	0	1	0	0
11		310	275	0	0	0	4	0
12	Dorsal + Left Ventral	343	248	1	0	0	0	2
Totals		9168	5343	14	31	151	4	3

* For marking zones and site locations see Figure 10.

way up the lake. While it appears from the data that shiners range the length of the lake, the data also indicate that they did not appear to move across the lake to any extent, at least during the time covered by this marking and recovery work. These figures imply that their movements at this time were confined to the shoal area and that they did not move across deep water. If they did move out into deeper water, they did not cross onto the opposite shoal to be taken in the traps on the south shore, and may have returned to the north shore.

The number of marked shiners caught in the area in which they were marked as compared to the number of these marks taken in other areas lent some belief to a gradual downstream drift or displacement of shiners. Six shiners were recaptured at the east end, which had been marked at the east end and four shiners marked here were recaptured in the west end area. In contrast to this is the fact that there were 135 west end marks recaptured in the west end but no recaptures of these marks in the east end or beyond the mid point of the lake. This seemed to indicate that shiners moved or were carried down the north shore to the west end of the lake and that there is only limited movement back up the lake from this area. There appears, from the data, to be more movement along the north shore than along the south shore. The shoals are much more extensive along the north shore. An attempt, in 1955, to trace lake currents which might have influenced a movement of this type bore no results nor does any other data corroborate this east to west drift implied in the 1952 data.

(ii) Horizontal movement across the shoal.

In order to test the hypotheses derived from the study of spatial distribution of shiners discussed above, an attempt was made in 1956 to follow any seasonal movement of the two size ranges across the shoal. The method employed, as described in "Details of Field Study," consisted of series of

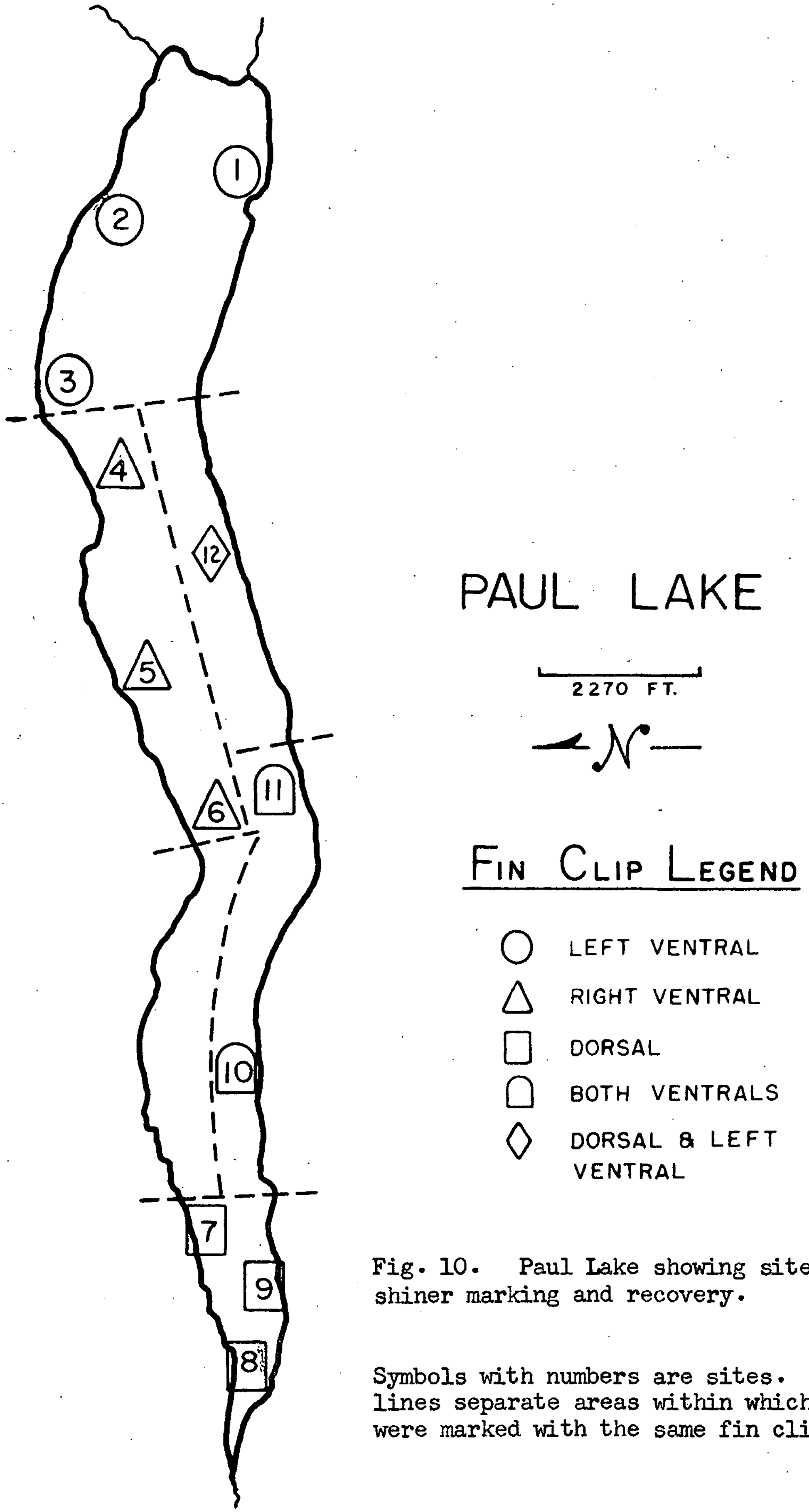


Fig. 10. Paul Lake showing sites of shiner marking and recovery.

Symbols with numbers are sites. Broken lines separate areas within which catches were marked with the same fin clip.

minnow traps at various locations, set at intervals across the shoal. The location of these sets are shown in Figure 2.

The data expressed in Figures 11a and 11b show the horizontal movements. More data, from May and September, may have illustrated the pattern more completely but the trend is shown. Figure 11a shows that while there are always more shiners at the shoal edge, decreasing catches in more shoreward traps are reflected in increases in offshore traps. As catches in Zone A decrease those in B increase and later when catches in B decrease, C increases. The peak in catches of Zone C traps (shoal edge) corresponds to the period of maximum surface water temperatures. The decrease in shoal edge catches and increase in mid-shoal catches corresponds to decreasing temperature on the shoals. The reverse movement with minimal temperatures on the shoal are not shown but derived from observations made by the author in late September and others in October and November. The lodge operator reports that just before the lake freezes over no shiners are to be seen on the shoals.

Work in 1955 also led to the belief that there was a difference between the movements across the shoal of large shiners ($2\frac{1}{2}$-4 inches) and small shiners (1-$2\frac{1}{2}$ inches). Figure 11b shows that while there are always more small shiners at the shoal edge there appears to be no definite seasonal shift of these shiners from shoal zone to shoal zone. The large shiners, however, carry out the trend gained from the plot of total numbers. The greatest numbers are inshore in June, midshoal in early July and then at the shoal edge (8-20 feet of water) when maximum temperatures are reached. These fish also show, to a small extent, the tendency to repopulate the shoal when shoal water temperatures decrease. Gillnets set in August took far more large shiners near bottom, at the shoal edge, than they did in June. Gillnet sets, at the time of maximum surface temperature, running along the bottom perpendicular to shore and from shoal edge to a depth of 45 feet showed concentrations of large

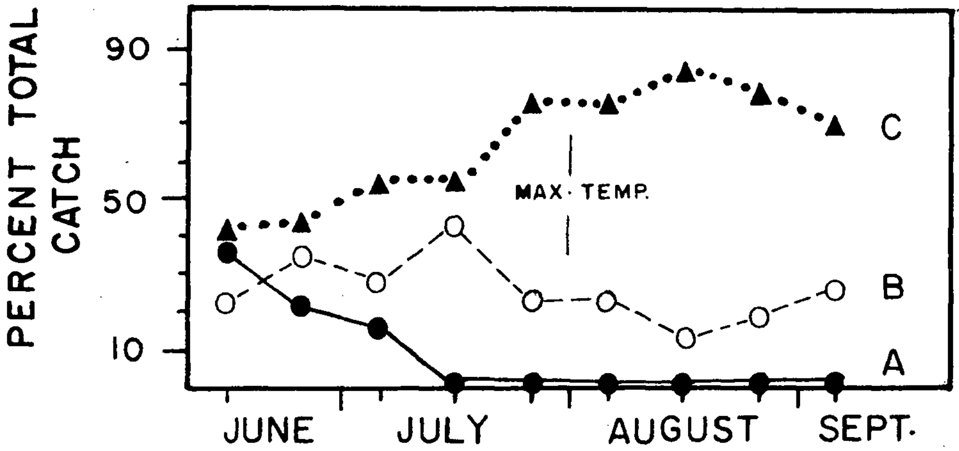


Fig. 11a. Catches of shiners in three zones across the shoal, for five day periods in summer 1956.

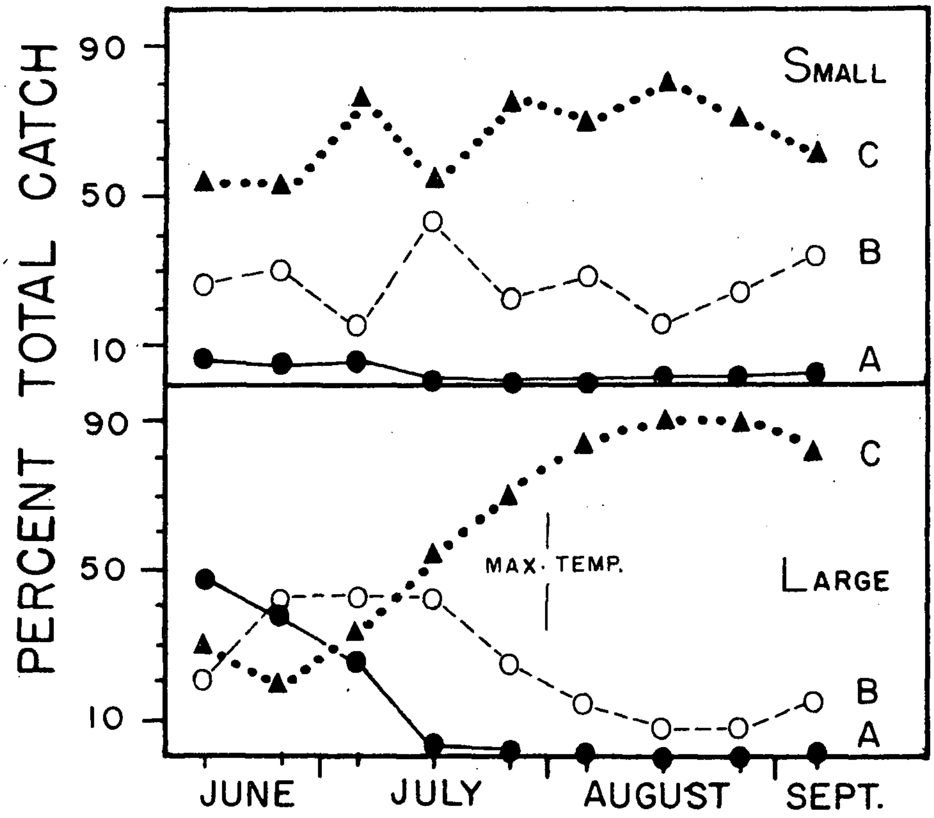


Fig. 11b. Catch of large and small shiners in three shoal zones in summer 1956.

A - Shoreline
B - Midshoal
C - Shoal-edge

Large - $2\frac{1}{2}$-4 inches (F.L.)
Small - 1-$2\frac{1}{2}$ inches

shiners in a narrow zone at a depth of approximately 30 feet. No shiners were taken in the net from the 30 to 45 foot depth and the number of large shiners decreased rapidly in that section of the net running up the shoal incline and onto the shoal. Direct observations in the fall of 1955 and 1956 showed that the large shiners disappeared first and the last shiners to be seen on the shoal were those in the one to two and one-half inch size range. It is thought that large shiners return to the 30 foot depth as the lake cools previous to freezing over.

(iii) Vertical movement at shoal edge.

Results of direct observations in 1955 implied a pattern in vertical movement of shiners at the shoal edge. To test the validity of this three minnow traps were set at shoal edge, one just above the bottom (20 feet) one at mid depth (10 feet) and the third one foot below the surface. These were emptied every other day, the total number and the number of large and small shiners at each depth recorded. It was more difficult to follow this pattern in that the response to temperature fluctuations seemed much more rapid. Figure 12a shows the total catch at each depth, for five day periods, from June 17 to September 19, 1956. Figure 12b indicates the catch of large and small shiners in these zones for the same period.

The curves illustrating the total catches describe the successive decrease in catch in shallow traps and the eventual concentration in the deep trap by the time of maximum water temperature on the shoal. As catches at the surface (trap C) began to decline in mid July, catches at mid depth (trap B) increased. The catch at the bottom (trap C) was also increasing and gained its maximum as that in B began to decline. The points for late August and September give some indication in movements toward the surface again and perhaps an eventual approximation of the points, similar to that in June, indicative of almost equal distribution in all depths.

When the catches are separated as to size (Figure 12b) no clear difference

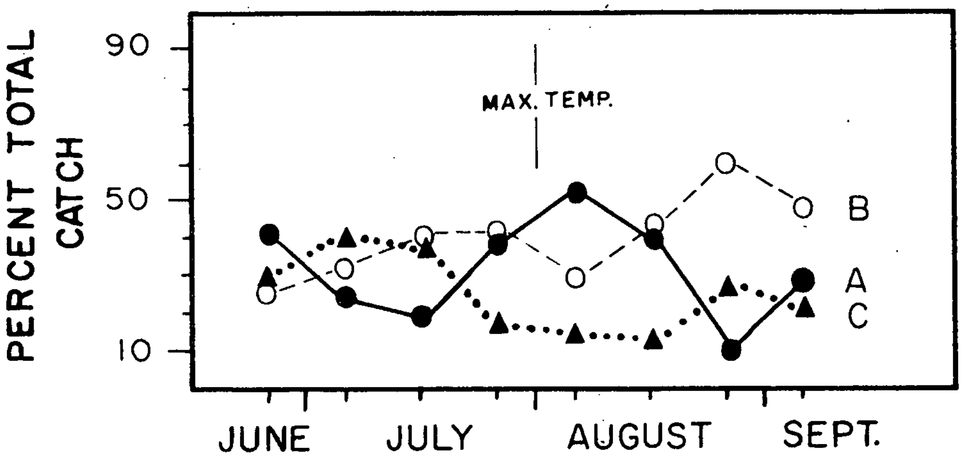


Fig. 12a. Catch of shiners in three depth zones at shoal-edge, for five day periods in summer 1956.

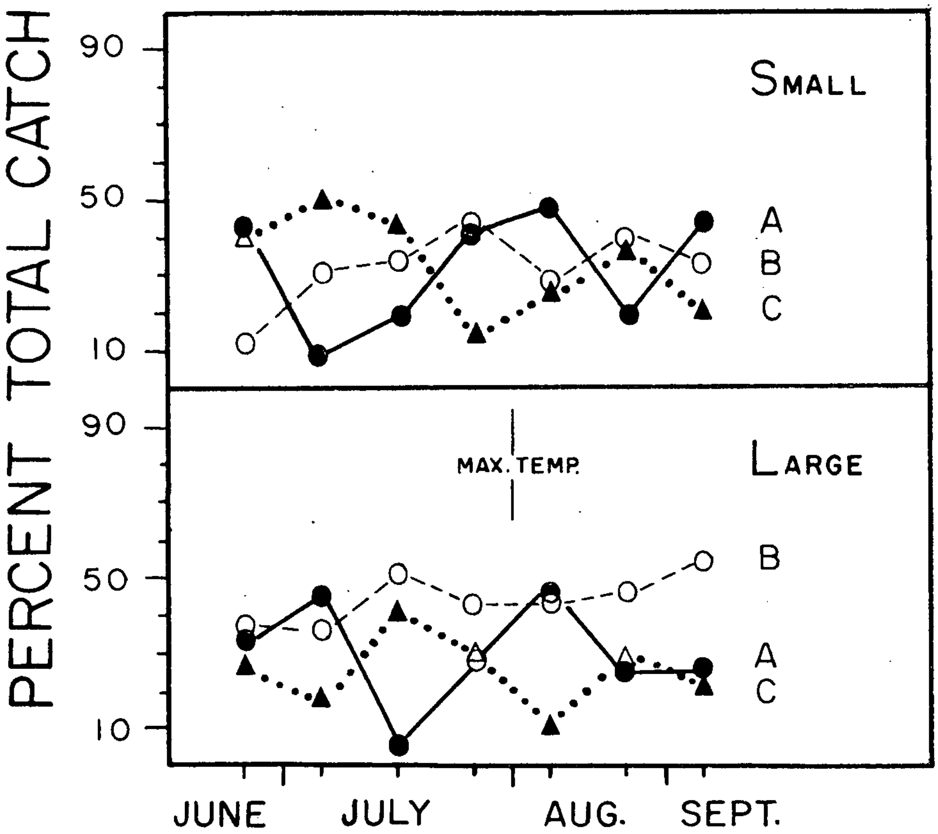


Fig. 12b. Catch of large and small shiners in three depth zones at shoal-edge, for five day periods in summer 1956.

A - Bottom B - Mid-depth C - Surface

in movement pattern for the two size ranges appears. The small shiners follow the general pattern, mainly at the surface in June, somewhat greater numbers in the mid depth and deep traps in late July and more even distribution in late summer. The only pattern visible in the catches of large shiners is their greater tendency to remain at mid depth and at bottom. This emphasizes the vertical stratification described in C(ii) above.

Both horizontal and vertical movements were first noted in 1955 when the lake level was constant throughout the summer. In 1956 when the attempt was made to follow this with traps, lake level dropped drastically exposing part of the shoal. It is possible that the complete pattern as seen in 1955, especially the repopulation of the shoal before the return to deep water for winter, was somewhat disturbed in 1956 by the decrease in depth of water over the shoreward portion of the shoal.

(iv) Diurnal movement.

In 1955 it was discovered that shiners were taken in overnight gillnet sets at lake centre over the entire length of the lake. It was assumed in 1952, from negative results of minnow traps set in vertical series in deep water, that shiners were restricted to the shoals. In 1955 gillnets set on the surface overnight caught 500-1000 shiners and lesser numbers at greater depths as described above. It was apparent that shiners either came up from deep water at the centre of the lake at night or moved out from shore. Since no shiners were seen in deep water in daylight hours and none were taken in gill nets below the limit of visibility, it seemed more likely that they moved out from shore. Direct observations indicated that no shiners were ever seen during daylight hours at any distance greater than 25 feet from the shoal edge. Shiners would follow a boat rowed across the shoal to this distance and then return to the shoal.

Gillnets were set on the surface at lake centre in the daylight and inspected at two hour intervals. Visibility was good (8-10 feet) and the area around the net was carefully scrutinized, each time, for shiners. No shiners were seen and none were taken in the nets during the day. Shortly after dark shiners began to appear in the nets. The net catches reached a maximum by 0400 hours and changed little from then until daybreak when the nets were removed. As described above, lake centre sets took shiners of all sizes and the vertical size stratification, so noticeable on the shoal, appeared to be maintained.

This change in the gillnet catch paralleled an observed offshore movement of feeding shiners. Shiners feeding on the surface are easily seen even in minimal light conditions. Feeding shiners, restricted to the shoal in the daytime, were observed to move out into deeper water as darkness approached. Places which had high concentrations of shiners during the day exhibited this and when these locations were inspected with a light after dark, shiners were absent or greatly reduced in number. Shiners were again abundant in these locations the following day.

Recaptures of marked shiners in 1952 gave some indication of a gradual drift of shiners, over the season, from east to west. This, coupled with the knowledge gained in 1955 of the offshore movement at night, led to the question of whether lake currents could be responsible for moving shiners from west to east at night when they lost contact with the shoal. With this in mind an attempt was made in 1956 to find any lake currents and to determine the extent of the offshore movement at night. The search for the lake current failed as a result of inadequate equipment and nature of the outflow of the lake. The lake is used to store water for irrigation and the outlet was at times wide open and at times shut tight for days.

More success was possible in tracing, to some degree, the extent of the offshore movement of shiners. In August 1956, shiners were caught by means of a purse seine, 100 feet long, and 18 feet deep. These were caught from a large school on the shoal just east of Swampy Point (closed square of Figure 5). Of the shiners caught, 14,300 of all sizes were marked by means of a fin clip and then released. After completion of marking seven pieces of gillnet ($\frac{1}{2}$-$1\frac{1}{2}$ inch mesh) were staggered at equal intervals across the lake. These nets were set parallel to shore from shoal-edge to shoal-edge in the marking area.

The total overnight catch of shiners in all meshes was 1,192. Of this catch, 11 were marked fish. The interesting point was that as many marked shiners were captured in the net set near the opposite shore of the lake as were captured in the net adjacent to the marking site. If we think of the pieces of mesh as A to G from the marking site to the opposite shore, Table IX shows the total number of shiners taken and the number of marked shiners recaptured. From this one can assume that at least some shiners cross the lake. It was impossible to tell whether they remained on this shoal or returned to the opposite shore. Gillnet catches at G two days later included no marked shiners.

It seems then, that redside shiners are distributed to a greater extent on the large shoals of the north shore of Paul Lake, than on the south shore. They exist as somewhat discrete schools of tremendous size separated by short intervals. They move to a certain degree along the shoals in an east-west direction and have a complicated movement pattern over the shoal which seems to relate to shoal water temperature. All of these factors, as shown in Figures 9, 11 and 12, tend to bring the shiners into contact with predatory rainbow trout during the months of July, August and September. This period corresponds to that in which shiners constitute a major portion of the diet of trout. Even diurnal movements which carry the shiners out into the centre of the lake and to a maximum depth of 25 feet may put them in a position in which they are preyed upon by trout.

TABLE IX

The total number of shiners taken, and the number of marked recaptures, in gillnets set at intervals across the lake parallel to shore.

Net Location *	Mesh size in Inches	Total Catch	Number of Marked Shiners
A	$\frac{1}{2}$, $\frac{3}{4}$, 1	418	3
B	$1\frac{1}{2}$	0 ✓	0
C	$\frac{3}{4}$	330	3
D	1	52	0
E	$\frac{3}{4}$	78	0
F	1	161	2
G	$\frac{1}{2}$, $\frac{3}{4}$, 1	153	3
Totals		1192	11

* A - adjacent to the marking site

G - adjacent to the shore opposite the marking site.

✓ Net sank to bottom.

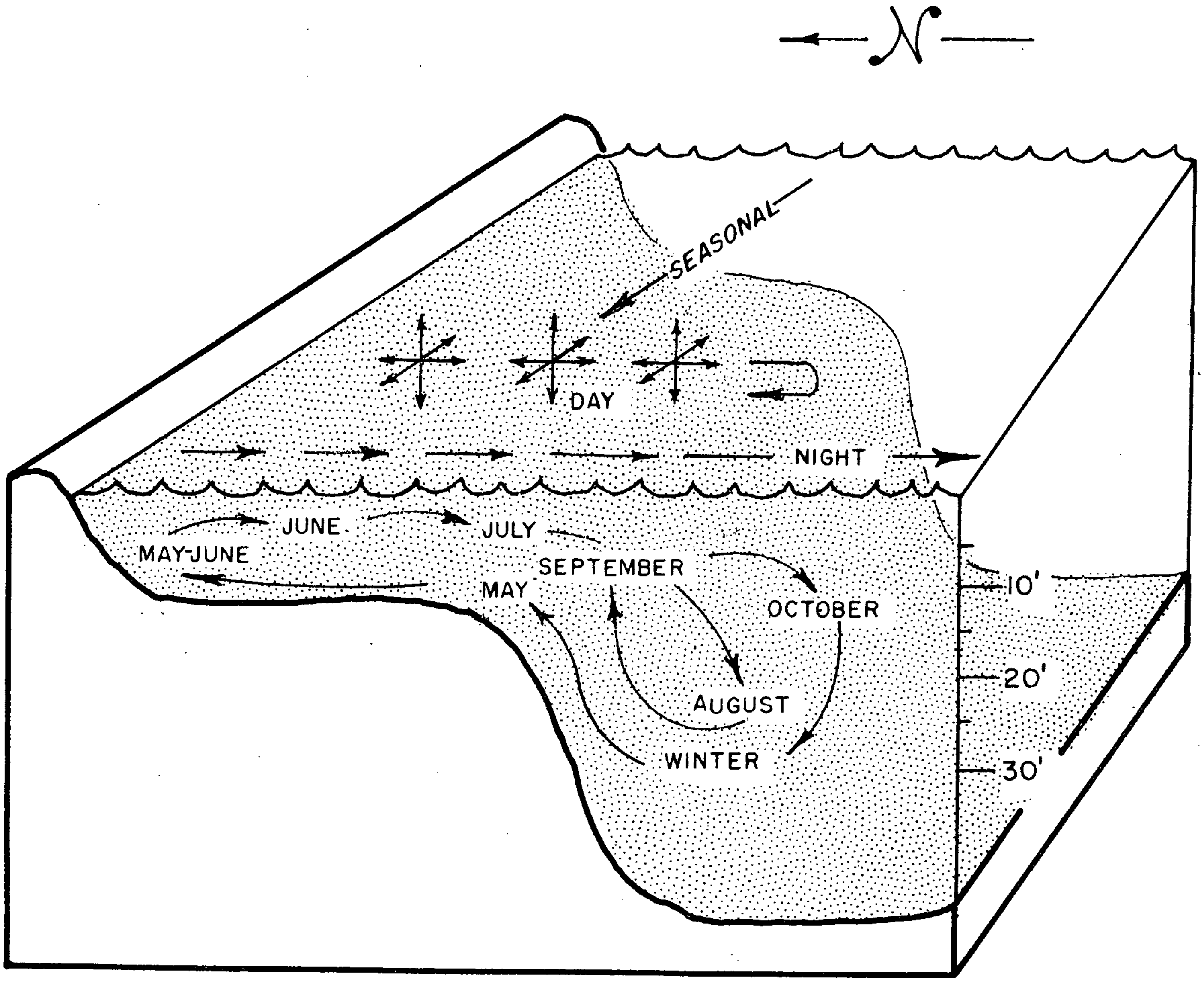

N
SEASONAL
DAY
NIGHT
JUNE
JULY
MAY-JUNE
SEPTEMBER
MAY
OCTOBER
AUGUST
WINTER
10'
20'
30'

Fig. 13.

Figure 13

Schematic representation of movement patterns of redside shiners in Paul Lake.

1. The cycle in the foreground represents seasonal movement over the shoal and the vertical movement at shoal edge. It is deduced that shiners spend winters off the shoals at approximately 30 foot depth. Large shiners are concentrated here in early spring. Shiners move on the shoal in mid May and have dispersed over the whole extent of the shoal by July. With maximum shoal water temperature in August they move off the shoal into deep water and return to the 30 foot depth. Decrease of water temperature in September results in partial repopulation of the shoal by shiners. At this time they rise closer to the surface at shoal edge. With approach of minimal temperatures shiners again disappear from the shoals and it is assumed they are to be found in deep water.
2. The arrows designating night pattern show the offshore movement at dusk. It is known that some shiners move completely across the lake. Whether they return by morning or remain on the other shore is not known.
3. The seasonal drift, along the shoals from east to west, at least as indicated for the north shore, is shown by the arrow in the background.
4. The multidirectional arrows over the shoal indicate random lateral and vertical movements over the shoal in daytime. The sharply recurved arrow at shoal edge indicates a tendency for shiners to go no farther than 25-30 feet beyond the shoal in daytime. Upon reaching this point they quickly turn about and return to the shoal.

ACTIVITY INVOLVED IN PREDATION

The factors affecting where and when predation takes place have been discussed above. It is also useful to know how predation takes place. There is, it seems, a difference in the degree of predation carried on by adult and juvenile rainbow trout in Paul Lake. In order to assess this the behaviour of these two groups when in contact with shiners is described below.

Adult trout, for this purpose, will be considered as being those over 10 inches fork length. Trout under 10 inches will be considered as juveniles for this discussion.

A. Behaviour of Adult Trout Preying on Shiners

It is possible that predation on shiners by adult trout takes two forms. One of these, to be described here, will be designated as surface or visible predation. This form is known to take place at certain times, in certain places and with a recognizable activity pattern on the part of the trout.

Surface or visible predation is known to take place over the shoals during the day. Visible predation by adult trout took place, according to observations in 1955 and 1956, only in restricted areas of the lake. This type of predation was seen only in the three following locations:

1. The shoal areas of the north shore portion of area BC and the extreme north-east portion of area DE (See Figure 5).
2. The south-east corner of Section A.
3. Just off Echo Lodge dock in Section H.

All of these areas are areas of extensive shoal but do not constitute the entire area of extensive shoal. No trout were observed taking shiners along the south shore except at the extreme east end of the lake. The south shore is almost entirely an area of very limited shoal. The only extensive shoal on the south shore is at the camping ground at No. 2 marker south. The great amount of boating and swimming activity at this point may prevent trout from preying on shiners there.

Many hours were spent, in the course of the study of the distribution of shiners, in areas where predation was observed to take place. Incidental to the distribution work direct observations were made, often close at hand, of trout preying on shiners. Repeated observations suggested a highly characteristic pattern of predation.

From a distance, the first signal of surface predation is a rippling sound, like rain falling on the surface of the lake, and the reflection of the silvery sides of shiners leaping out of the water. This is followed by two or three loud splashes made by a trout as it moved across the surface of the water pursuing the shiners.

In areas where the visible predation could be observed more closely, the trout could be seen swimming in from open water at a depth of about 6-8 feet. It was commonly possible to identify the trout by means of marks, scars, injured fins, etc. Characteristically, the trout would swim slowly by under the school of shiners and swim off, out of sight, into open water. This passage of the trout caused no apparent alarm on the part of the shiners two to three feet above it. The trout would soon return at the same depth but at far greater speed. Close to, or under the school of shiners, the trout would rise toward the surface. It was during this rise that the shiners would disperse and leap out of the water. The trout would rise to the surface of the water and there would be two clearly audible splashes in close succession as if the trout thrust with its tail very vigorously first to one side and then to the other. While on the surface it would engulf a shiner, or sometimes one and then another one. At times the trout would chase a shiner over the surface six or eight feet before capturing it. Then it would dive to an approximate depth of six to eight feet and return to open water.

In all cases observed the trout appeared to be pursuing individual shiners rather than attempting to catch one at random by rushing through the centre of the school. Typically the trout came to the surface at the edge of the school, rather than in the centre of it. It was commonly observed that around the fringe of a large school of shiners, there would be five to ten, three to four inch shiners, that were less active than the others and somewhat isolated from the main group and that these shiners were the victims of predation. It was apparent from all observations made, that, contrary to a common anecdotal observation, trout did not come up into the school, stun shiners with its tail and then turn and engulf injured prey.

All trout observed feeding in this manner appeared to be over 12 inches in length and many of them appeared to be in the 16-20 inch size range.

From observations in 1955 it seemed that many appeared very dark in colour as if sexually mature. Analysis of all fish known to have eaten shiners showed that more were not sexually mature than were so. Out of a total of 783 trout examined in 1955, 627 showed no sexual development and 156 showed some signs of sexual maturity. Of this total of 783 trout, 128 had shiners in their stomachs. Considering only the 128 trout which had eaten shiners 76 showed no signs of sexual maturity and 52 trout showed some signs of maturity. Signs of maturity were maturing gonads or spent ovaries and spawning colouration of spawned-out females.

In 1956 intensive visible predation began only after mid June and appeared to be at the peak of intensity from late July to mid August. While in 1956 it continued up to termination of field work on September 17 it was less intensive after late August. Notations were made each day that predation was observed to be taking place. A crude estimate of intensity either in number of trout seen, or in degree of predation (such as light medium or heavy) was also made. Light intensity signifies fewer than 25 instances of trout

TABLE X

Intensity of predation in summer months 1955-1956

	Range of Dates of Observations	No. of Observations	Intensity
May	30	1	1 trout only
June	15	1	2 trout only
July	10-31	13	heavy
August	2-23	13	med. to light
September	3-17	5	light to med.

Intensity is number of times in a day visible predation was observed.

Light	-	less than 25
Medium	-	25 - 50
Heavy	-	over 50

preying on shiners, medium intensity 25 to 50 and heavy over 50 instances in any one day.

Table X shows this data. Heavy predation was listed only in July. Predation in August was listed as ranging, chronologically over the period of observations, from medium to light. In September the intensity ranged in the opposite direction, light at first and then somewhat more intensified at the termination of field studies.

It was also observed that on clear, hot days in July and early August when the lake was extremely calm, predation was at its heaviest. On these days visibility through the water was exceptional and the reflection of the sun off the silvery scales of a shiner was clearly visible at 25 to 50 feet. This reflection may have made the shiners more readily detected by trout.

B. Behaviour of Juvenile Trout with Shiners

One important facet of the whole predator-prey association of rainbow trout and redside shiners is that shiners constitute a small portion of the diet of small trout. This is so, even though, during the time shiners constitute 90 percent of the diet of large trout, newly hatched shiners, of a size which small trout can utilize, are abundant.

Small trout (4-6 inches) although not often seen, when seen in the lake were always in company with a school of shiners. There appeared to be no interspecific aggression. The shiners, however, appeared to be more efficient feeders, and when a trout and shiner darted after the same food item, the shiner invariably got it and while shiners would move right into the shore to feed, trout appeared to come only into water no shallower than 15 inches.

Field observations led to the question of whether the definite size stratification of shiners, described in the distribution section, isolated small trout from the small shiners. Simple unrepeated trough experiments, designed to determine whether small trout (4-8 inches) were capable of catching and eating small shiners and whether the presence of large shiners would deter them from this, were carried out in the winter of 1955-1956. Trough experiments, conducted at the Institute of Fisheries which involved holding 4, six inch trout with varying numbers of shiners of various sizes showed the following: The trout seem to establish territories in the corners of the troughs but they moved about freely with the shiners. In the troughs as in the lake the shiners were more active feeders. Vertical size stratification of shiners was apparent here also.

Trout ate no live, active shiners during the first week, during which time all fish were fed hatchery food. They did, however, try unsuccessfully, several times, to engulf one inch shiners which were killed and introduced similarly to other food.

However, after a starvation period of one week in which trout received no food, four six inch trout held with 20 one to one and one-half inch shiners did eat shiners. In four different trials they ate shiners at a mean rate of 0.14 shiners per trout per day.

In other experiments six inch trout were held with equal numbers of large and small shiners and with greater numbers of large than small shiners. In these experiments large shiners in no way appeared to prevent or lessen the contact of trout with the smaller shiners. The trout not only ate small shiners at a rate approximately equal to the other experiments, but apparently killed some of the larger shiners.

It appears that, at least under experimental conditions, the presence of large shiners (nearly as large as trout used) did not prevent small trout from preying on small shiners. Trout four to six inches in length are not only capable of eating small shiners but under conditions of prolonged starvation appear to have attacked and killed shiners almost as large as themselves.

EXTENT OF PREDATION

Of the questions to be answered as outlined in the introduction to the study, those of where, when and how predation takes place have been dealt with above. In order to answer to what extent predation takes place, an analysis was made of the contents of the stomachs of 1603 trout from the anglers' catch of 1955 and 1956. These will be used to demonstrate the seasonal change in diet, the importance of shiners in the diet and the way in which the degree of predation on shiners divides the trout into size groups.

In order to trace the development of predation by rainbow trout on shiners in Paul Lake, the 1955 and 1956 data are compared with that for the period 1946-1949 and 1952 as summarized in Larkin et al (1950) and Larkin and Smith (1954).

The introduction of shiners into Paul Lake from the lakes above it in the chain has had considerable effect on the diet of trout in Paul Lake. According to Larkin et al (1950) in the period 1946 to 1949 there were no significant differences according to size in the diet of trout over eight inches in length. In these years amphipods (Gammarus and Hyalella) contributed substantially to the large quantities of bottom organisms taken, particularly in the spring and early summer. Plankton comprised roughly two-thirds of the diet in July, August and September. No fish were observed in the stomachs of trout taken in the years 1946-1949.

Larkin and Smith (1954) state that by 1952 radical changes had taken place in the diet. Amphipods had become a negligible food source for all sizes of trout. From July to September fish was the main item of food for trout over 12 inches long, constituted a substantial proportion of the diet of trout from 10 to 12 inches and was recorded occasionally in the stomachs of trout from eight to ten inches long. Shiners taken by trout were almost always relatively large, and shiner fry were rarely found in trout stomachs. The food habits of the smallest fish (8-10 inches) remained relatively the same as in 1946-1949 but trout over 10 inches replaced plankton with fish as the main food source in July, August and September. In the larger trout (over 14 inches) fish made up more than three-quarters of the diet in July, August and September.

A. Relative Volumes of Various Food Items in Summer

Stomach volume data from 1955 and 1956 show an extension of this same pattern in that there appears to be a gradual increase in the amount of fish consumed. The relative importance of shiners in the diet readily divides the trout into three length groups (6-10, 10-14 and 14-14+ inches F.L.) in regards to diet. This is quite different from the period from 1946-1949 when no clear difference was exhibited in the diet of trout of various sizes. Table XI shows the percentage volume of various food items, for trout of these three size groups, for May to September, 1955 and 1956. This table is an extension of Table I of Larkin and Smith (1954), which summarizes the same type of data from 1946-1952.

Figure 14 shows the change in percentage volume for the three main diet items from 1946-1956 for three size groups of trout in Paul Lake. Shiners have increased and plankton decreased almost proportionately. It is interesting to note that although shiners appeared in Paul Lake in 1945, none were seen in the stomachs of trout until 1950. Bottom organisms show a great increase since 1952 in the middle size range as a result of the decrease in importance of a fourth item, surface insects, which were of greater importance previously. The bottom fauna in 1955 and 1956 was composed mainly of dragonfly nymphs,

TABLE XI

Average volume of stomach content of rainbow trout according to month and length group in 1955 and 1956. Number in bracket under length group is number of trout in that group for whole year. Number in bracket beside month is the number of trout of all sizes in that month.

YEAR	Length Group (F.L. in.)	ITEM	MAY (23)					JUNE (222)					JULY (271)					AUGUST (171)					SEPTEMBER (107)				
			Shiners	Plankton	Bottom Organisms	Surface Organisms	Misc.	Shiners	Plankton	Bottom Organisms	Surface Organisms	Misc.	Shiners	Plankton	Bottom Organisms	Surface Organisms	Misc.	Shiners	Plankton	Bottom Organisms	Surface Organisms	Misc.	Shiners	Plankton	Bottom Organisms	Surface Organisms	Misc.
1955	6-10 (198)	Number of stomachs with item	-	-	1	-	-	1	10	23	2	1	1	49	7	1	1	4	53	15	1	-	-	15	16	-	-
		Percentage with item	-	-	33	-	-	3	26	61	5	3	1	89	13	1	1	6	75	21	1	-	-	48	52	-	-
		Percentage of total volume	-	-	100	-	-	1	15	80	1	3	1	69	24	2	4	9	66	22	3	-	-	48	52	-	-
	10-14 (490)	Number of stomachs with item	-	1	15	1	-	14	72	90	1	4	23	143	35	2	-	11	40	28	2	-	6	15	30	-	2
		Percentage with item	-	5	79	5	-	8	43	54	1	2	12	78	19	1	-	15	55	38	3	-	12	30	61	-	4
		Percentage of total volume	-	3	93	4	-	9	16	73	1	1	22	45	32	1	-	32	31	36	1	-	20	15	62	-	3
	14-14+ (117)	Number of stomachs with item	-	-	2	-	-	6	4	18	1	3	14	13	18	-	1	15	10	5	3	1	17	2	13	3	-
		Percentage with item	-	-	100	-	-	21	14	64	4	11	42	39	55	-	3	56	37	19	11	4	63	7	48	11	-
		Percentage of total volume	-	-	100	-	-	7	3	86	1	3	39	6	54	-	1	88	4	6	2	-	73	3	21	3	-
	Total	Number with item for year	0	1	18	1	0	21	86	144	4	8	38	205	60	3	2	30	103	48	6	1	23	32	59	3	2
1956	6-10 (106)	Number of stomachs with item	-	-	5	-	-	-	3	10	1	5	5	21	5	-	6	2	16	19	-	1	2	20	16	-	1
		Percentage with item	-	-	100	-	-	-	18	59	6	29	19	79	19	-	22	7	59	70	-	4	7	67	53	-	3
		Percentage total volume	-	-	100	-	-	-	14	58	-	28	22	49	25	-	4	6	33	61	-	-	14	45	40	-	1
	10-14 (439)	Number of stomachs with item	5	23	132	1	20	13	29	81	1	18	35	56	33	3	8	38	22	20	3	5	6	10	24	2	2
		Percentage with item	4	17	96	1	14	12	28	78	1	17	34	55	33	2	7	60	35	32	5	8	19	31	75	6	6
		Percentage total volume	2	2	95	-	1	11	15	71	-	3	62	17	20	-	1	79	5	14	1	1	19	12	68	1	-
	14-14+ (253)	Number of stomachs with item	-	7	26	-	4	26	17	50	2	19	30	15	19	2	4	51	6	14	2	4	14	8	17	2	-
		Percentage with item	-	27	100	-	15	33	22	63	3	24	57	28	36	4	8	81	10	22	3	6	44	25	53	6	-
		Percentage total volume	-	1	98	-	1	29	7	58	-	6	74	4	20	-	2	94	1	4	1	-	67	2	29	2	-
	Total	Number with item for year	5	30	163	1	24	39	49	141	4	42	70	92	57	5	18	91	44	53	5	9	22	38	57	4	3
			MAY (169)					JUNE (190)					JULY (182)					AUGUST (153)					SEPTEMBER (94)				

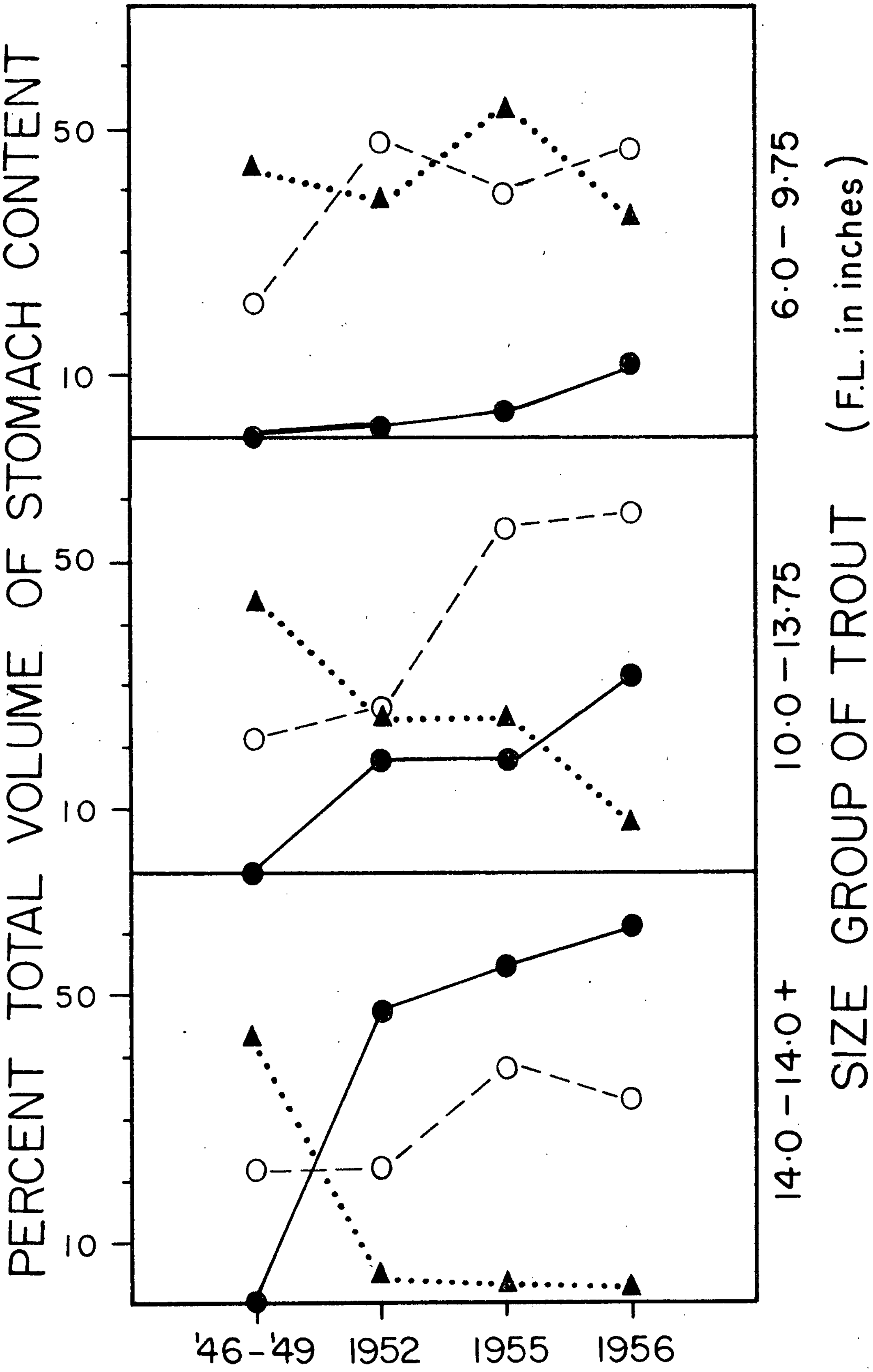


Fig. 14. Percent total volume of stomach contents, for three size groups of trout, of shiners (●), plankton (▲) and bottom organisms (O).

Data for 1946-1952 from Larkin and Smith (1954).

snails and chironomid pupae. Even individual gammarids were rarely present.

Seasonal variations in the diet are much the same for each of the size groups of trout, the change in importance of various items merely occurring at a different time or to a different level in the different size groups of trout. Since 1952, bottom organisms have comprised over 80 percent of the diet in May and over 60 percent in June. The previous dominance of plankton in the diet in July, August and September, now found only in the small trout, has been replaced by a dominance of shiners in the large trout and bottom organisms in trout of the middle size range. Figure 15 shows the seasonal variation in percentage total volume of stomach contents for the three most important items in the diet of trout 10.0-13.75 inches (F.L.) in 1952 and 1956. This figure shows the change to dominance of bottom fauna and shiners since 1952 and the decrease in the importance of plankton. This change in seasonal variation of food types is best demonstrated in this size group, which includes the size at which trout are thought to begin largely feeding on shiners. Twelve inches appears, from all evidence, to be the approximate size at which trout begin feeding on shiners. Larger trout had established, by 1952, the beginning of the importance of shiners in the diet. Shiners, in that year, constituted 79 percent of the stomach contents of fish over 14.0 inches in August and September. In August 1956, 94 percent of the volume of stomach contents of trout of this size group was shiners. While there is an increase since 1952 in the volume of shiners consumed by large trout, it is not as noticeable as the increase in the 10 to 14 inch trout. The diet of the smallest size group, while showing an increase in the amount of shiners consumed, is still dominated by bottom organisms and plankton as it was previously to 1952.

Figure 14 compares the percentage total volume of stomach contents for these same food items, by size groups, in 1952 and 1956. It shows the

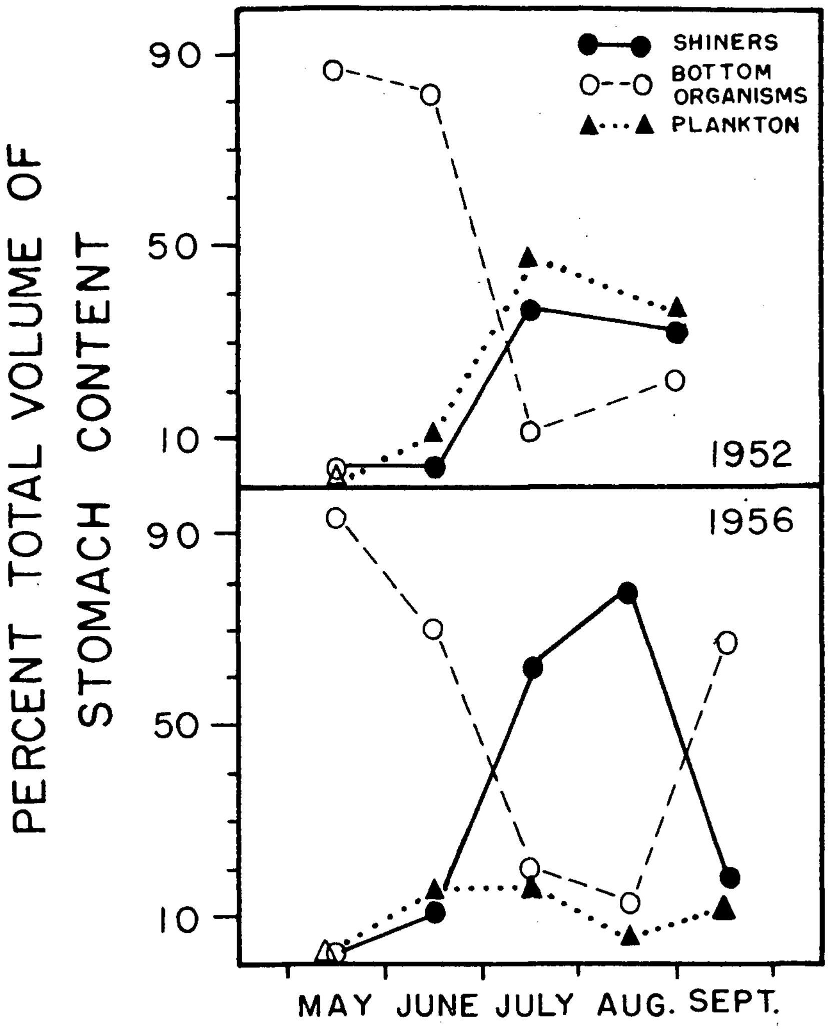


Fig. 15. Seasonal variation in the contribution, of shiners, plankton and bottom organisms, to the diet of rainbow trout 10.0 - 13.75 inches (F.L.) in 1952 and 1956.

1952 data from Larkin and Smith (1954).

relationship between size of trout and volume of shiners consumed and the decreased contribution of plankton to the diet of trout over 10 inches. While it shows increases in amount of shiners consumed for all sizes the increase shown for 6-10 inch trout is very significant. For the other two size groups shiners had by 1952 assumed significant proportions. The rise in the smaller trout from such a low level in 1952 is perhaps indicative of the fact that size at which trout begin to prey on shiners is gradually decreasing.

The increasing importance of shiners in the diet is further emphasized by the fact that the yearly average stomach contents of rainbow trout in Paul Lake have increased, for that size group over 14 inches, from approximately 1.5 c.c. in 1946 to 6.5 c.c. in 1952 and to 7.9 c.c. in 1956 (see Figure 16). The middle size range shows an increase of 1 c.c. but the small trout show no increase in the average volume over 1952 and the 1956 average is actually lower than in 1947 when the shiners had not, as yet, become well established.

The 1955 data show that the volume was made up of as many as five larger shiners, or as in a single case, 21 smaller shiners.

It appears that, for trout less than 14 inches in length, while shiners are assuming a somewhat larger proportion of the diet, they are not increasing the average stomach volume and probably do not constitute a factor in increasing the growth rate. However, the increasing importance of fish in the diet of trout over 14 inches and the resulting increase in average stomach volume of almost 7 c.c. in 10 years, is probably affecting the growth of this group of trout quite strongly.

Also apparent is the fact that bottom fauna is the most stable food source in Paul Lake, since it constitutes never less than 20 percent of the total volume all through the summer, and never less than 83 percent in the winter.

B. Relative Volumes of Various Food Items in Winter

The data up to 1952 do not include any stomach samples of trout taken in

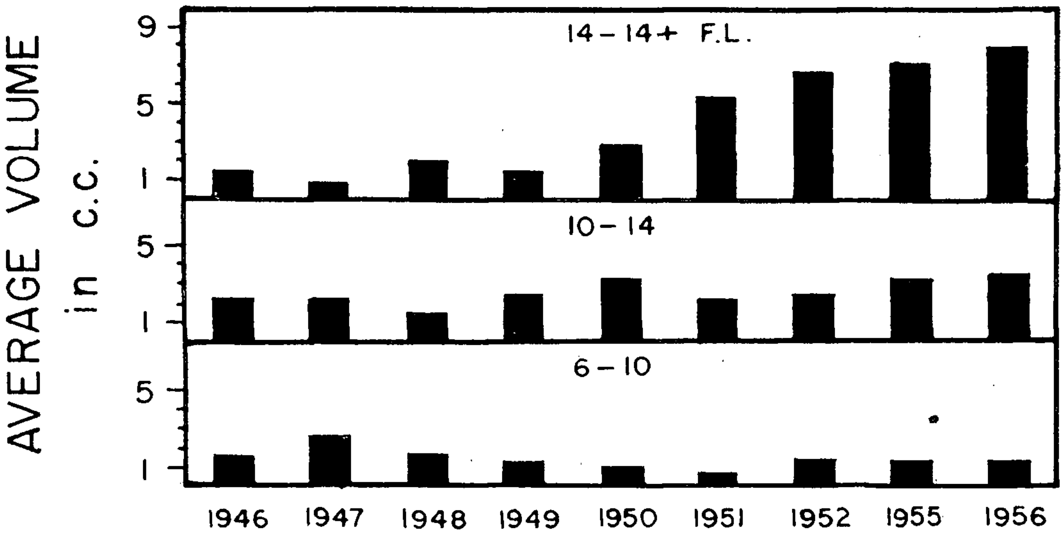


Fig. 16. Average volume of stomach contents of rainbow trout from Paul Lake, 1946 - 1956.

Data from 1946 - 1952 from Larkin and Smith (1954).

the winter. However in the winter of 1955-1956, 86 trout were taken in gill-nets and the stomach contents analyzed. These samples show complete dominance of bottom fauna in the winter diet of all sizes of trout similar to that observed in the spring and early summer. Bottom fauna constituted 94 percent of the diet for the smallest trout, 93 percent for the middle size range and 83 percent for the largest trout.

Shiners are of far less importance in the winter diet than in the summer diet. They did not enter into the winter diet of the four samples of 6-10 inch trout that were obtained. Shiners constituted only 0.1 percent in the middle size range (10-14 inches) and this was made up from a single stomach in the group of 46 trout of this size. Even for the largest trout, the diet of which is so largely shiners in the late summer, shiners comprised only 10 percent of the food. The proportion of shiners in the total diet of this group of trout is this high only by virtue of the fact that it is made up of one stomach (out of a total of 26) which contained the relatively high amount of 25.7 c.c. of shiners.

C. Size of Trout and Size of Shiners Preyed On

Table XII gives a comparison of the size of shiners preyed on by various size trout. It indicates that the maximum size utilized to any large extent is three to four inches. The number of four to five inch shiners eaten drops to three as compared to 74 for three to four inch shiners. The modal size is two to three inches. This is the smallest segment of the group considered as large shiners in the discussion of the movement of shiners.

The data show a direct relationship of size of trout and size of shiners eaten. By far the greatest part (79 percent), of the shiners eaten by trout over 18 inches, are over three inches in length. In fact 60 percent of shiners eaten by trout over 10 inches in length are over two inches in length.

It appears then that large trout prey, to the largest extent, on the large size group of shiners and utilize small shiners to a negligible extent. The section on the movement of shiners emphasized that it was these large shiners which were moving off the shoals into deep water in areas BC and DE during the time when large trout appeared to be moving into these areas.

As is indicated in Table XII, even trout in the six to ten inch category, when they do prey on shiners, prey on shiners over one inch in length. They do not utilize the abundance of shiners of one-half to one inch in length.

The discussion above, on the relative volumes of various food items, emphasizes the predatory pattern built up from the distribution and movement data. It shows the gradual increase, over the years, in the amount of shiners in the diet of all trout. The amount of shiners in the diet reaches a maximum of 95 percent, for trout over 14 inches, in August 1956. Analysis of seasonal variation in relative volumes, places the peak in the importance of shiners in July and August. It is at this time that all sizes of trout show the highest degree of predation. For comparison, volume of stomach contents for all sizes of trout in 1956 were converted to values for a standard size (mean length of the sample). These corrected volumes show peaks in May and August. The May peak is composed of the bottom organism dominance and the August peak of shiners. This standard comparison shows monthly average stomach contents in August to be 4.5 c.c. as compared to 2.8 c.c. in June, and 2.9 c.c. in July. The May peak is represented by 3.9 c.c. and the average for the first half of September is 2.9 c.c.

The monthly mean number of shiners preyed on (for all sizes of trout) in 1955 was highest in August. In that month the average number of shiners eaten was 2.9, it was 1.5 in July, and 1.6 in September. Increased volumes of shiners consumed in August probably consist of greater numbers of shiners and of shiners of the larger size range. This peak in amount of shiners in the

TABLE XII

Size of shiners consumed by various sizes of trout in 1955 and 1956.

Trout Size (F.L. Inches)	Shiner Size (F.L. Inches)				
	½-1	1-2	2-3	3-4	4-5
6 - 10	1	3	2	-	-
10 - 14	13	31	62	10	-
14 - 18	1	8	30	33	1
18 - 23	-	3	6	31	2
Totals	15	75	100	74	3

diet corresponds to the peak offshore movement of large shiners as shown in Figure 11.

The volume of shiners consumed, or degree of predation, readily divides the trout into three size groups. Trout six to ten inches prey on shiners very little. It is thought that predation begins in the 10-14 inch size group and Table IX shows that it is in this group that the greatest size range of shiners is preyed on. Trout over 14 inches show the greatest volume, and the largest size, of shiners consumed. There is further evidence that these trout feed almost exclusively on shiners in late summer. In Paul Lake when trout are angled using shiners as bait, figures for the size of trout caught and the volume of shiners in their stomachs are significantly larger than those figures for trout caught by anglers using standard tackle. A random sample of 35 trout angled with standard tackle was compared with 35 trout angled with shiners. The mean size of anglers' trout was 16.6 inches while the mean size of trout angled with shiners was 18.2 inches. A chi square test of the two size distributions showed a significant difference ($p = <.01$). The mean total stomach volume for trout angled with shiners was 25.2 c.c. and the mean volume of shiners in the stomachs of these trout was 25.1 c.c. as compared to means of 12.1 c.c. and 11.3 c.c. for trout angled with standard tackle. A "t" test of the difference in volume of shiners in the stomachs of the two groups of trout showed a significant difference ($p = <.01$).

The catch per unit of effort, using shiners as bait during July and August (periods of heavy predation), is considerably higher than that for standard methods. The catch per man hour, as numbers of trout is doubled (0.9 as compared to 0.18), and as weight of trout is nine times (1.6 as compared to 0.18) that of standard angling methods in July and August.

EFFECTS OF PREDATION

In any discussion of predation a factor of utmost importance is the effect of the predator on the prey and any effect of the prey on the predator. Predator control programmes usually have as their major objective the eradication of predators which supposedly hold the population of some desired animal at a level lower than the habitat may be capable of supporting. The effect of predator, as control, on the numbers of prey is the prime concern.

In the case of trout and shiners in Paul Lake, the predator is the desired animal. It is useful, however, to make some estimate of the effect of trout on shiners. To trout in the small size range shiners constitute a serious factor of competition for food. In the case of large trout in Paul Lake shiners constitute a major part of their summer food. The question arises as to whether the predatory activity of large trout acts as a control on the number of shiners and in this way might gradually reduce the competition exerted on small trout. This will be discussed as the effect of trout on shiners.

Similarly the change, over the years, in the diet of trout, the increase in the consumption of shiners and the competition exerted by shiners, has changed the growth rate of trout in Paul Lake. This will be discussed as the effects of shiners on trout.

Each of these factors is of considerable importance in any consideration of management policy for this lake, and other bodies of water containing trout and a competitive non-game species.

A. Effect on Redside Shiners in Paul Lake

Larkin et al (1950) give an estimate of the population of two-year-old and older trout in Paul Lake as at May 1, 1950. It is possible to calculate proportional strength of various size groups in the population from a catch curve (Ricker 1948) of the 1955-1956 anglers' sample. Combining these data one can make a crude estimate of at least the order of magnitude of various size groups at the mid point of a hypothetical season.

Using these data it is estimated that at mid season there were approximately:-

12,500 trout 6-10 inches

2,490 trout 10-14 inches

855 trout 14-14+ inches

The size groups are chosen to correspond to the stomach analysis data.

From the stomach analyses it was determined that the degree of predation, measured as the number of trout in the sample which had eaten shiners, varied between the size groups. In the total anglers' sample of trout in 1955 and 1956, of those trout 6-10 inches in length 0.05 percent had eaten shiners, 16.3 percent of trout between 10 and 13 inches had preyed on shiners and 46.7 percent of the large trout had shiners in their stomachs.

Applying these percentages to the estimated number of trout indicates that, in the hypothetical season, the number of trout in each size group in the sample which had, on any one day, eaten shiners can be considered as:-

625 trout 6-10 inches

406 trout 10-14 inches

399 trout 14-14+ inches

The total number of trout which had on any one day eaten shiners was 1,430 out of an estimated total population of 15,845 trout over six inches in length. Any control on the number of shiners in the lake, in the form of predation by trout, is being exerted by less than nine percent of the trout population on any particular day.

It is known that, for those trout in the sample which had preyed on shiners, the mean number of shiners found in the stomach was 1.7. The highest number recorded was 21 small shiners in an individual stomach. This is an isolated case and no others were as high as 10 shiners. This mean is for all sizes of trout but is derived mainly from the large trout. When size groups are separated the mean numbers of shiners found in the stomachs of trout, in 1955-1956, are 1.2 in 6-10 inch trout, 1.8 in 10-14 inch and 2.5 for trout 14-14+ inches in length.

It is also known, from experiments with live trout in captivity, that it takes at least 24 hours for a single shiner to completely pass through the stomach.

The period of intensive predation seems to extend from about July 1 to late September according to the study. This would establish the length of the season of predation at about 82 days.

The percentage of the anglers' sample of trout which had shiners in their stomachs, as stated above, will be assumed to represent the percentage of each size group which had, on any one day, preyed on shiners. This figure with the data for mean number of shiners consumed by trout in each size group and the length of the predation season can be utilized to calculate the seasonal mortality of shiners as a result of predation by trout. Table XIII gives these figures for the three size groups.

The seasonal loss of shiners as a result of predation by trout is estimated to be of the order of 148,500.

The population of shiners in Paul Lake is extremely large and their number difficult to estimate. Lindsey (1953) describing a fin marking experiment with shiners in this lake, states that the total number of shiners proved too great for adequate population estimates. He goes on to say however, that Paul Lake probably contained between 5000 and 100,000 shiners per acre prior to the spawning period in 1950. Expressed as total population these limits would be 5000,000 and 100,000,000. Larkin and Smith (1954) cite another marking and recovery experiment involving 1,913 yearling and older shiners in June 1952. They state that local movements of shiners make assumptions of random mixing of marked individuals from different trapping areas impossible.

TABLE XIII

Estimate of the number of shiners preyed on by trout in a season.

Size Group of Trout (F.L. in Inches)	Estimated Number in Lake	Percent Anglers' Sample containing Shiners	Estimated No. Preying on Shiners on any One Day	Mean Number of Shiners Eaten	Number Eaten By All Trout in Size Group in 82 day Season
	(a)	(b)	(ab)	(c)	82 x (ab) x (c)
6 - 10	12,500	0.05	63	1.2	6,199
10 - 14	2,490	16.3	406	1.8	60,582
14 - 14 +	885	47	399	2.5	81,795
Totals	15,875		868		148,576

These authors estimate the population of shiners in the vicinity of each trap at approximately 15,000 individuals and based on the area each trap fished, state that the shiner population of Paul Lake probably comprised several million individuals in 1952. Even considering the lower limits of these crude approximations, it appears that trout predation does not act as an effective control of the number of shiners in the lake. Larkin and Smith (1954) conclude this to have been the case in 1952 saying:-

> "It is doubtful whether predation by the present trout population would significantly affect the numerical abundance of the shiner population of Paul Lake. Since the large stock of Kamloops trout in Paul Lake did not deter the multiplication of the first few immigrant shiners it most certainly would make little inroad into the present population of several millions."

The failure to deter the multiplication of the first few immigrant shiners might be attributed to the small probability of the meeting of trout and shiners at that time. However, figures for estimated kill at present, when stomach contents of trout indicate a high degree of predation, still constitute no control of the number of shiners.

Another fact to be considered is the type of shiner that is preyed upon by trout. It is important to include the life history stage of the animal preyed on in order to estimate the effect, on prey population numbers, of the predator. From Table XII it is known that over 60 percent of the shiners eaten by trout are over two inches in length. Only five percent of shiners eaten are fish of the year. From the discussion of the seasonal variation of degree of predation the fact is apparent that the heaviest predation is in August when most of the spawning of shiners is over.

In other words, the greatest percentage of predation is exerted on that part of the population not contributing to recruitment to the stock of shiners. Young fish of the year are not eaten. Those large shiners taken, quite possibly have spawned and may die before the next spawning season. In this way predation by trout is neither limiting recruitment of young shiners to the population nor reducing the large numbers of mature shiners before they have an opportunity to reproduce.

B. Effects on Rainbow Trout in Paul Lake

The relationship of the two species of fish in Paul Lake has changed since 1945. After a meteoric rise in numbers of shiners, predation and competition exerted by these fish brought about a drop in production and decrease in the growth rate of trout in Paul Lake by 1952. At this time predation by trout on shiners was low. The change in 1953, to stocking the lake with larger trout ended the loss, at least in those trout artificially recruited to the stock, as a result of predation by shiners. It also reduced the time between periods when trout were a size at which competition with shiners was severe and the size at which trout fed on shiners.

Gradual increase in the degree of predation, reduction in size at which shiners constitute an important part of the diet, and increase in the stomach volumes of larger trout may be evidence of partial compensation, in larger trout, for the inhibitory action impressed on smaller trout as a result of competition from shiners. The apparent increase in the number of large trout (four to six pounds) in the anglers' catch may be the combined result of the known success of liberated trout and any increased growth rate as a result of feeding on shiners. Larkin et al (1957) state that availability of food organisms determines the ratio of energy gained from food intake to energy expended in living processes. Trout eating shiners take in more food than those not eating shiners. In a sample of 815 trout in 1955, 134 had eaten shiners and 681 had not. The seasonal, average corrected stomach volume for those trout eating shiners was 4.3 c.c. while for those not eating shiners it was 2.0 c.c. This increase in food intake as a result of ready availability of food, in the form of shiners, should be reflected in growth rate.

Growth of fish expressed as "Size Specific Instantaneous Annual Growth

Rate" (Larkin et al 1957), compares growth on the basis of size rather than age. Since size is so important as a determinant of the way in which an animal meets its environment, this technique better describes the effect of environment on growth. Expressed in this way growth rate of trout makes possible an insight into one of the effects of shiners on trout in Paul Lake.

Figure 17 shows the instantaneous growth rates, in relation to fork length, for trout in Paul Lake for three periods. The period 1946-1949 represents the lake before the entrance of shiners, 1952 the time when shiners were exerting maximum influence and 1955-1956 a time when predation by trout on shiners was an important feature. While the effect of competition is still visible in the depressed growth rate of small trout, as compared to 1946-1949, that for the 1955-1956 period is somewhat higher than for 1952. The fact that the 1955-1956 line crosses the 1946-1949 line in the eight to twelve inch size range is some indication that growth rate, for trout over eight inches in length, may be greater than in the period when the lake contained trout only. The four to five year age maximum for trout and extremely variable growth rate makes it impossible to calculate size specific growth rates for sizes over 12-14 inches. The effect on growth rate might be much greater at these larger sizes.

Examination of larger trout which had eaten shiners indicated that weight was an important feature. The larger trout appeared very deep and thick. It is possible that the main increase in growth as a result of feeding on shiners is expressed in weight and will not be too apparent in growth rates using lengths only. The growth curve for 1955-1956, combining weight and length, might be much higher, for larger trout, than even the 1946-1949 curve.

Mention has been made above of the interval between 1945 and 1950 when, although shiners were present in the lake, shiners were not found in the stomachs of trout. The somewhat stereotyped behaviour of trout preying on shiners has

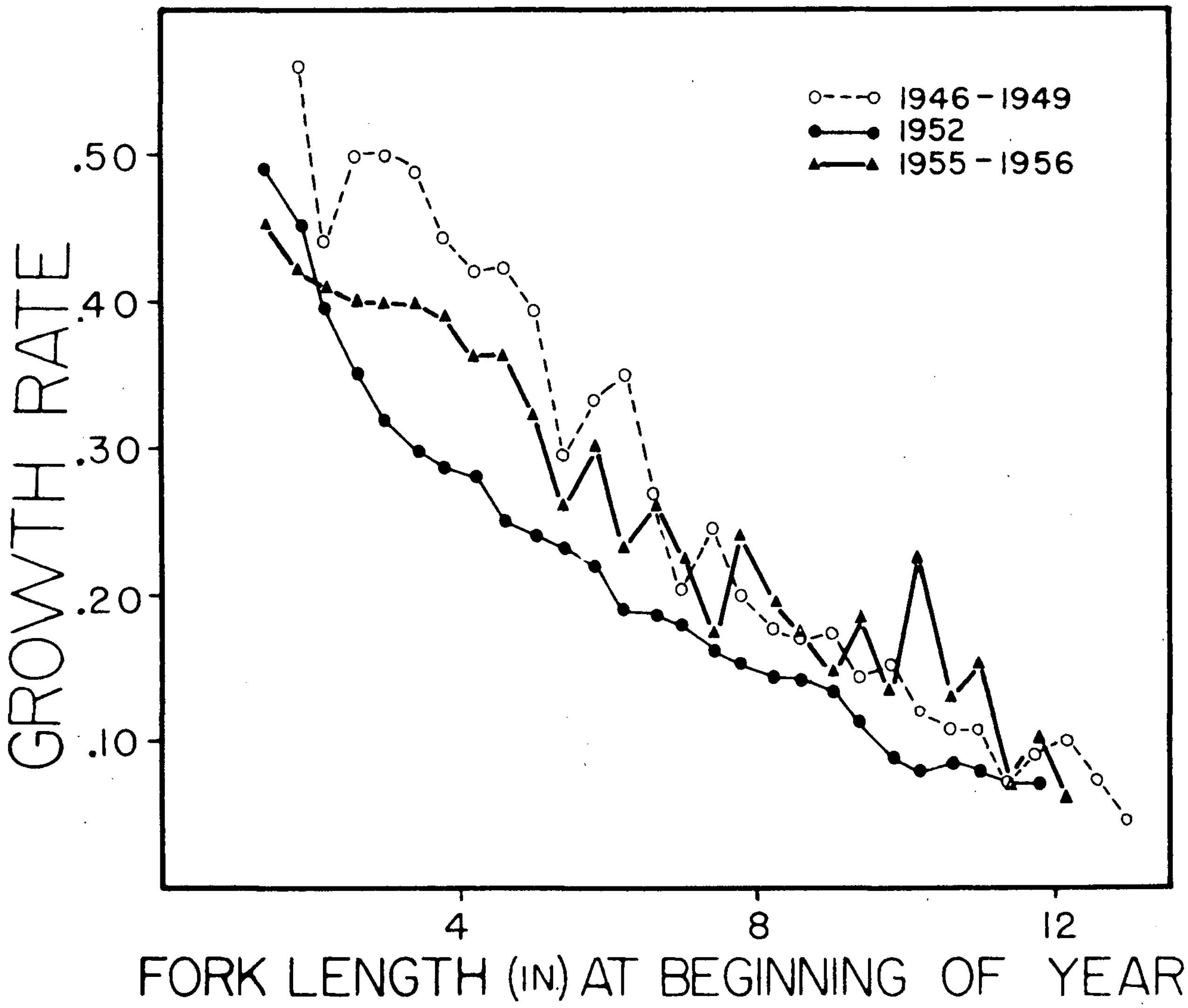


Fig. 17. Instantaneous growth rate ($\log_{10}$ fork length at age $_{n+1}$ minus $\log_{10}$ fork length at age $_{n}$) in relation to fork length at the beginning of the year for rainbow trout in Paul Lake before and after the introduction of the redside shiner.

1946 and 1952 curves from Larkin et al (1957).

also been described.

These two facts suggest the necessity of a period of time for the change from omnivorous to piscivorous food habit. The effect, of difference in length of lake residence in contact with shiners, for comparable size trout, on the degree of predation on shiners would also emphasize this point. Marked liberated trout have at least one and maybe two years less resident time in the lake than unmarked trout of similar size. Unmarked trout have had one or two additional years in contact with shiners and other trout feeding on shiners. Table XIV compares the mean volume of shiners consumed by marked and unmarked trout in 1955 and 1956. It shows that in both 1955 and 1956, (except for 10-14 inch trout in 1955) that marked trout of all sizes ate smaller quantities of shiners than did unmarked trout. This is especially true for the largest trout where the figure for unmarked trout is double that for marked trout.

Increase in amount of shiners consumed with longer lake residence is apparent also when marked fish are followed through successive years. Table XV shows the average volume of shiners consumed in 1955 and 1956 by trout liberated in spring of 1954 and by trout liberated in spring of 1955. This increase from 1955 is partly an artifact of progression of trout from one size range to a larger one. There is, as described above, an increase in volume of shiners consumed, with size of trout. These data may however, emphasize that of Table XIV showing an increase in amount of predation with increased lake residence.

TABLE XIV

Volume of shiners consumed by marked and unmarked trout
in 1955 and 1956.

		6.0 - 9.75			10.0 - 13.75			14.0 - 14.0+		
		No. of Trout	Total Volume of Shiners	$\bar{X}$ Volume	No. of Trout	Total Volume of Shiners	$\bar{X}$ Volume	No. of Trout	Total Volume of Shiners	$\bar{X}$ Volume
1955	Marked	49	0	--	184	62.1	0.3	23	25.7	1.1
	Unmarked	149	8.4	0.06	416	118.8	0.2	94	418.7	4.5
1956	Marked	15	0	--	166	113.8	0.7	85	224.7	2.6
	Unmarked	91	15.8	0.2	273	421.7	1.5	168	1004.3	5.9

TABLE XV

Volume of shiners consumed by marked trout in successive periods after entry into Paul Lake.

	1955			1956		
	No.	T. Vol.	$\bar{X}$ Vol.	No.	T. Vol.	$\bar{X}$ Vol.
Trout liberated in 1954	112	83.8	0.1	62	148.1	2.4
Trout liberated in 1955	43	0	0	194	190.4	0.9

SUMMARY

Time, place, manner and extent of predation on redside shiners by rainbow trout in Paul Lake are all dependent on several somewhat complicated factors involving the distribution and movement of the two species of fish, size relationships and behaviour.

Predation on shiners by trout, a phenomenon which appears to have developed only after the two species had been together in the lake for five years, has increased since 1952. It occurs extensively only in late June, July, August and early September. Predation appears to be most intense on hot calm days when water is calm and visibility very good.

Movements of both trout and shiners, perhaps in response to water temperature, tend to concentrate the two species in the same areas of the lake during summer months. These are areas of extensive shoal. In fact the intricate seasonal pattern of movements of shiners across the shoal, at the shoal edge and possibly the diurnal movement to open water bring shiners into places in which they can be preyed on by trout. In July shiners are concentrated on the shoals. This coincides with a time when water temperatures are below maximum and when trout can make short excursions into this shallow water. It is at this time that visible predation is so noticeable. At this time shiners constitute approximately 50 percent of the diet of trout over 14 inches in length. In August, when water temperature is highest, the shiners move off the shoal into deeper water, visible predation is less obvious and shiners constitute approximately 95 percent of the diet of trout over 14 inches in length.

Adult trout preying on shiners appear to do so with a definite pattern of behaviour at least during the time when predation is visible at the surface. While trout under six to eight inches in length are often found with shiners

of a size they are capable of eating, these trout utilize shiners to a negligible extent.

The volume of shiners in the summer diet of trout has been steadily increasing since 1952.

There is a definite relationship between size of trout and volume of shiners eaten. In 1956 shiners constituted a maximum of 22 percent of the diet of trout six to ten inches in length, 79 percent of the diet of trout 10 to 14 inches in length and 94 percent for trout over 14 inches.

There is a seasonal variation in the degree of predation. In the summer months the volume consumed is lowest in May and June. Volumes rise sharply in July and August and decline gradually in September. This variation conforms to the movement pattern of shiners. Peak predation occurs when the shiners are in 10 to 20 feet of water at the shoal edge. Predation is less intense when shiners are in shallow water on the shoals and in winter when they are presumed to be in deeper water (30 to 40 feet). In winter shiners form an insignificant part of the diet of trout. At this time the diet of all sizes of trout is very similar to what it was before shiners entered the lake.

A direct relationship exists between size of trout and size of shiner preyed on. Over 60 percent of all shiners eaten by trout over 10 inches in length were over two inches in length. Shiners smaller than this are utilized to a far less extent.

The effects, of the predator-prey relationships, on these two species of fish in Paul Lake are manifold. These fish exist as reciprocal competitors and predators. The effect of predation by shiners on small trout has been lessened by the liberation of larger trout. Competition has perhaps not decreased.

As a predator rainbow trout are estimated to kill approximately 148,500 shiners per season. The total population of shiners in the lake is estimated at several millions. It seems unlikely that predation exerts any control on the number of shiners in the lake.

From 1949 to 1952 competition from shiners decreased production and depressed the growth rate of trout in Paul Lake. In 1956 growth rate of trout was still below that for the period when trout alone utilized the food resources of the lake. There is some indication of compensation for this in the growth rate of trout over eight inches in length. Ready availability of food in the form of shiners, for those trout which are piscivorous, seems to elevate the growth rate slightly above that for 1946-1949. It is difficult to show this for the size range in which trout prey so heavily on shiners. It is also apparent that weight must be taken into consideration when attempting to evaluate the effect of predation on the growth rate of trout.

DISCUSSION

While the study outlined above constituted a particular situation on a single lake, factors involved in it have application to two broad principles. The Paul Lake data will be discussed below, as it applies to the phenomenon of predation, and in relation to management of sport-fish lakes containing these two species of fish.

It is a general characteristic of communities of fish populations that predator-prey situations are temporary rather than permanent in nature (Ricker 1952). Most species that are piscivorous as adults have alternate sources of food such as bottom organism, in addition to which most predacious fish have juvenile stages in which plankton and bottom fauna are the chief food sources (Langlois 1954). Predation is typical of certain ages (or sizes) of piscivorous species; is typically influenced by seasonal factors, and in many situations involves several species of prey fishes (Larkin 1956). The predation of rainbow trout on redside shiners in Paul Lake is thus fairly representative of common predator-prey relationships in fish populations. Rainbow trout feed on shiners only after attaining a certain size, predation is seasonal, the predator is not entirely dependent on the prey for food. The degree of predation is influenced by many factors, including variations in temperature of shallow water and climatic conditions, behaviour of trout and shiners and relative availability of different types of food.

It is impossible to say at present whether the relationship of this predator and this prey is always such as has been demonstrated for these two species in Paul Lake. The importance of environmental factors would lead one to believe that the relationship of even these two species would vary with differing habitat conditions. Paul Lake is oligotrophic (Rawson, 1934), in a eutrophic lake such as Pinantan, the lake above Paul in the chain, temperature and oxygen conditions in the epilimnion and hypolimnion may be such as to maintain the two species in contact over a greater period of the year than in Paul Lake.

Lake morphometry which did not lend itself to shoal development might create an entirely different picture of the movement and distribution of the two species. Difference in the extent and distribution of Chara in different lakes could change the relationship.

The similarity of the interaction of these two species, in other lakes as compared to Paul Lake, is at present under study. It is almost certain each species combination in each habitat may exhibit entirely different factors governing their interaction. It is reported (Carl and Clemens 1953) that other salmonids such as cutthroat trout (Salmo clarki Richardson), Dolly Varden (Salvelinus alpinus malma (Walbaum)) and lake trout (Salvelinus namaycush (Walbaum)) are more piscivorous than rainbow trout. These salmonids might show entirely different interaction even in closely similar habitats. The young of these species might be important predators whereas only adult rainbow trout seem to be.

In Paul Lake, numbers of trout are primarily determined by climatic factors and aspects of intraspecific competition, rather than by the availability or abundance of shiners. The numbers of shiners is scarcely influenced by predation by trout and the relationship between the two species does not afford an opportunity for density dependent predation over the full range of potential prey densities. In consequence the relationship between trout and shiners, which is typical of situations in freshwater communities, bears little resemblance to the existing theoretical models of predation.

Theoretical models of predation fall into three general types; the earlier ones referred to as the Lotka-Volterra models and more recently the Nicholson-Bailey models and Ricker's predation situations.

The Lotka-Volterra models are based on a derivation of the "Logistic Law."

This law is a mathematical expression of the idea that in a limited space the potentially possible geometric increase of a given group of individuals at every moment of time is realized only up to a certain degree depending on the unutilized opportunity for growth at this moment (Guase 1934). Lotka-Volterra models treat simultaneously the effect, on the rate of increase of predator, of the addition to the population of individual prey organisms and the effect on the increase of prey of each additional predator. Effect of predator is converted to represent the dampening effect on increase in number of prey which the addition, to the prey population, of a certain number of prey (calculated to be equivalent in effect to one predator) would have. Effect of prey is calculated as added unutilized opportunity for increase, as compared to rate of increase of predators without prey.

When we say that growth of predator and prey populations may be represented by logistic curves and when these equations are solved simultaneously, among the implied provisions are the following:-

(a) That the populations have stable age distributions at the start.

(b) That for each species the relationship between density and rate of increase is inversely proportional; that is, that the rate of increase is decreased by a proportional amount for each individual added to the number already present in unit space; and that each individual has the same effect as each other individual, on the numbers of its own population and that each individual has the same effect as each other individual on numbers of the other population.

(c) That the depressive influence of density on rate of increase operates immediately i.e. that the rate of increase is slowed down as soon as each additional animal is added to the population, and that each individual affects its own and the other population immediately.

Stable age distributions are probably not found in either the trout or shiner populations of Paul Lake. Age distribution of trout is compounded chiefly from success of spawning migrations and intensity of angling. Age distribution of shiners is erratically influenced by predation by varying numbers of trout preying on only certain sizes of shiners.

The simultaneous solution of two Lotka-Volterra equations implies that not only is provision (b) correct for both species but that each individual prey or predator has the same effect on numbers of prey or predator regardless of age or size. The restricted nature of the size range of shiners preyed on in Paul Lake shows unequal contribution of individuals of the prey species. The variation in degree of predation of the different size groups of trout denotes an unequal effect of individual predators added to the situation. Each predator added as a young rainbow trout may feed on a stock of food other than the prey until it reaches a certain size. Rate of increase may be density dependent in shiners but it appears that other factors neglecting angling, such as water flow in spawning stream play a greater role in determining the number of trout in the lake. The inequality of contribution of each animal added to the situation seems to be inherent in most predator-prey situations. This is especially so in those situations involving animals with complex life-histories and life-stages requiring different habitat, food, temperature etc.

The third premise of logistic equations, that the effects of addition of individual prey or predators are reflected immediately in rate of increase or decrease, is also unsatisfactory in application to the present data. There is no evidence that predation by trout on shiners is immediately or even eventually reflected in any increase in the numbers of trout. Nor is it likely that a decline in abundance of shiners would be followed by a decrease in numbers of trout.

These are only some of the assumptions which Lotka-Volterra models must fulfil in order to validate their basis in logistic law. In addition qualities inherent in the hypothetical animals of the models, such as insatiability, infallability and randomness of movement, make these animals seem distant from nature and would seem to limit the application of these models to simple organisms in closely controlled situations. The type of predation that occurs between trout and shiners would appear to be much less intense than would be necessary to satisfy Lotka-Volterra equations. Predation is only a casual factor, rather than a causative factor in determining abundance of the two species. It may perhaps be a distortion to suggest that the population dynamics of the two species are intimately tied to their inter-relationships. The same general criticism can be applied to the suitability of the Nicholson-Bailey equations which require an obligate type of predator-prey relationship.

The Nicholson-Bailey models are built around two basic concepts, the "competition curve" and the "steady state" derived algebraiclly from qualities of hypothetical animals in the models. The competition curve relates the density of the pupulation of predators to the proportion of previously undiscovered prey found by each predator. The steady state embodies particular values of the densities of interacting animals such that density of prey is just sufficient to maintain the predator and density of predator is sufficient to destroy the surplus of hosts. When the densities have these values the theory implies that they must remain constant indefinitely in a constant environment.

The hypothetical animals of the Nicholson-Bailey models are obviously patterned on entomophagus parasites. These writers repeatedly use the general term "animals" but the models depict such specialized "predators" that this alone limits the application of this type of model. Nicholson-Bailey animals have the following characteristics:

(a) The predator does not devour the prey, this is done by the following generation.

(b) Ease with which prey can be found does not vary with the density of the population.

(c) While individual predator may be highly specialized to seek out prey the predator population searches at random.

(d) Appetite of predator is insatiable irrespective of the density of the prey.

(e) The predator has two characteristics referred to as "areal range" and "area of discovery" which are involved in the search for prey. Constant values for these two, as would be required for a mathematical description, imply that the predator searches for prey with the same efficiency irrespective of prey density.

The main limitation of this type of model was the choice of an obligate, perhaps species-specific, entomophagous parasite as the animal on which to base the assumptions. The characteristics of such a highly specialized animal surely cannot apply to all predator-prey situations. It leaves no room for versatility of the predator in the way of food utilization. Winter and summer diets of trout in Paul Lake indicate that trout might be described as omnivorous apparently turning to whatever food is most readily available to them. One can infer from seasonal and yearly variations that this change is not a regular or cyclic alternation of foods but depends on what food is at hand in the greatest amounts. Some larger predators seem to be bound more closely to a smaller choice of alternate foods but are not dependent on a single species.

In Paul Lake the degree of predation seems to vary directly with the concentration of prey in areas accessable to trout. Shiners in winter appear to be distributed in such a way that they are not preyed upon as heavily as in summer when they are concentrated at the shoal edge. That is to say the predator does not find the same proportion of prey irrespective of "density."

If in summer water temperature conditions tend to bring the two species in close contact, then perhaps the predator population does not "search" at random.

Nicholson (1954) states that the application of Nicholson-Bailey equations was from the first explicitly restricted to predators of the entomophagous parasite type and their hosts. Nicholson in this paper goes on to say that equations in the 1954 paper can be modified to describe more precisely the equilibrium conditions for any particular kind of animal. The writer feels, however, that the equations in the 1954 paper as well, have too specific a relationship to specialized insects to be of universal application.

Nicholson ends the 1954 paper by saying that no equation could conceivably be produced which takes into account explicitly all factors known to influence populations. He says that only a few factors influence any given population significantly and the effects of these can be expressed by using relatively simple equations. While mathematics is a form of shorthand expression one must avoid too readily dismissing seemingly remote factors for the sake of ease of expression or mathematical manipulation. The possible complex role of behaviour, a factor almost beyond mathematical formulation, in the predator-prey relationship of trout and shiners in Paul Lake points this out.

This phase of the predation problem in Paul Lake constantly arose as an enigma. A study of the role of animal behaviour in predator-prey relationship might lead to the revelation of more of the subtle factors involved in these complex relationships. A closer scrutiny, more carefully documented, of the behaviour of adult trout preying on shiners, the role of calm sunny days as they apply to reflection or silhouetting of prey, detection by predator and degree of predation would be of great value. Another study which suggested itself was the role, of behaviour of small trout with various sizes of shiners, in the apparent absence of predation by small trout. The description of factors such as these and others involved in the behaviour of predator and prey might make it more apparent that predator-prey interactions do not lend themselves to universal expression.

Ricker (1952 and 1954) discussing what he calls predation situations describes three seemingly natural sets of circumstances involving mechanisms of predation. They seem very apt descriptions of typical relationships and make no assumptions about outcome in regards to relative numbers of predator and prey. In two of these he utilizes fish as examples. These situations depend on the assumption that predation is the only cause of death of the prey over the whole period. The period cited is "season." It is difficult to imagine a natural situation in which mortality over a whole season could be attributed to predation alone. He also says that many predacious fish must set up that type of predation situation in which they can take whatever food they encounter as often as they encounter it and rarely find prey so abundant that any must be refused. It seems implicit in the Paul Lake evidence, that while the predator-prey relationship closely resembles that described by Ricker, that it would be possible for trout to encounter prey more often than the number of prey found in stomachs would indicate they do. Ricker also stresses the importance of the ability of the predator to increase in number as a direct result of the increase in the number of prey. This does not appear to be the case when so often number of predators is governed by factors other than food. Ricker does describe the likelihood for prey to "slip out from under" by becoming so numerous that predation does not control their numbers. This, it appears, is what has happened in Paul Lake.

In the Ricker situations as in the Lotka-Volterra and Nicholson-Bailey models, the mathematical approach seems to be founded too strictly on particular relationships or animal complexes to be a universal expression of an ecological phenomenon which appears to be the result of a multitude of closely intermeshing factors. The casual rather than causative effect of the complex interaction of predator and prey suggests that to isolate this phenomenon is to look at only one of many interrelated phenomena, of which nothing less than the additive or multiplicative effects express the total of the ecological association of freshwater communities.

A second important consideration of the data on the relationship of rainbow trout and redside shiners in Paul Lake is in regard to ecology and management of sport fishing lakes. The sport fishery on lakes such as this is dependent on the production of trout and this in turn is dependent on the ecological relationship of all the animals (and plants) in the lake. The difficulty encountered, in lakes which contain sport fish and "coarse fish," is the fact that while the food resource is shared by both groups, only the sport fish are considered desirable. Economic production of these lakes is measured in pounds or numbers of sport fish only.

Describing food relationships of animals, Elton (1927) discusses the role of "key industry organisms" in utilization of primary foods and the build-up of primary foods into units more suitable for larger animals higher in the food chain. A partial solution to the problem of food utilization in mixed fish populations would be possible if the niche of coarse fish in lakes was that of key industry organism and the desirable species was an efficient and constant predator. Theoretically, in this way the abundance of bottom organisms could be efficiently cropped by the shiners and the shiners used as food by the trout.

Some of the areas of Paul Lake, such as the shoals which are highly productive of food, are accessable to trout for only limited periods of the year. Temperature of shallow water in summer possibly limits the time trout can spend on shoals browsing on small organisms. Shiners can better tolerate these higher water temperatures and are quite probably more efficient than trout in reaching organisms dispersed within the vegetation. This, no doubt, was the possibility which led Lindsey (1950b) to say, of the relationship of the redside shiner to production of trout in British Columbia, that it might be possible, knowing the role of each major species, to manipulate management measures so as to turn the presence of shiners from a liability to an asset.

One must consider, however, the connection between the many factors involved in the relationship of these two species and the production of trout in Paul Lake and other lakes having similar conditions. Among these are growth of trout, angler preferences and cost of various management measures.

It has been shown that growth of trout under eight inches in length is depressed below the level of years when trout alone utilized the food resources of Paul Lake. There is some indication of a partial compensation for this in increased growth in trout eight to twelve inches in length. It is also surmised that this compensation might be greater if weight was taken into consideration and if the technique used to compare growth in various years was capable of showing that for trout larger than 12 to 14 inches.

The criteria for management of sport fisheries are arbitrary and often more than one alternative is available. Angler preferences, fishing techniques and ethics, attached by anglers to sport fishing, change. Often the choice of management technique has to take these factors into consideration.

The type of fishery to which lakes such as Paul Lake are subjected may be referred to as a "family fishery" rather than a "trophy fishery." The family is now the angling or boat group. Angler preference at present is for a fishery that will yield quantity and high catch per unit of effort rather than the possibility of large trout requiring long hours of slow fishing, and low catch per unit of effort (measured as number of fish). Optimum production of trout for this type of fishery is a large number of trout from 12 to 14 inches with a weight of one to two pounds. Again the number of trout is emphasized. Trout of this size produced as yearlings and harvested within a minimum of time during which the fish are subjected to natural mortality would seem to yield the best possible production from the angler's standpoint. At present growth rate in Paul Lake is such that trout cannot be harvested as yearlings to the extent they were before 1949. Effective management at present necessitates annual liberation of trout three to four inches in length which have been maintained in a hatchery for one year before liberation. This has been a very successful interim policy and improved fishing in spite of competition from shiners. It is, however, a costly expedient. The growth period at which trout could best be harvested is below the limit at which maximum advantage of shiners as food seems to be achieved. It seems then that while shiners may increase the size and number of larger, older trout available, the point on the growth curve where this takes place does not correspond to the point at which best yield is possible.

Another consideration is the attitude and preference of the angler for certain types of angling. It is hard to change long-standing preferences and these are, as far as trout fishermen are concerned, for flyfishing and trolling. Rawson (1934) pointed out, that there was little reason to suppose that introduction of minnows would improve the production of trout in Paul Lake and that it might harm the fly fishing by supplanting insect material in the diet of trout. This appears to have happened as fly fishing is not as successful now as formerly. Evidence mentioned above seems to indicate that possibly the only way to harvest the larger trout (15-22 inches, 3-6 pounds) is by still-fishing with shiners. This method is not only not favoured by most anlgers but involved the grave danger of transport of live shiners to other lakes not containing this species, in an attempt to achieve the success this method yields in Paul Lake. The time lag between introduction of shiners into Paul Lake and their significant entry into the diet of trout makes it doubtful that shiners as bait would show any immediate increase in success in lakes containing only trout. This possibility alone, however, would not prevent the contamination of other lakes as a result of dumping unused shiners.

The other favoured angling method is trolling with artificial lures such as spoons. This method, it is suspected, selects faster growing fish as soon as they reach legal size limit. While the size limit has been removed in British Columbia this selection may still be effective on trout within the size range where growth is depressed by competition with shiners. Greater success trolling might be achieved with younger, faster growing trout.

If shiners were absent from Paul Lake, or drastically reduced in number it is possible that the lake could support itself. Since fish cultural activities are no longer carried out on the only productive spawning stream and since the number of adults in the spawning run has increased natural production in the spawning stream might be sufficient without predation and competition from shiners. If, as is likely, it is necessary to continue annual liberations the lake could be stocked with trout fry rather than yearlings. This would decrease the cost of liberations. Taking into consideration the difference between fry and yearlings survival from liberation to anglers' basket, the cost of trout in the creek is calculated at 60 dollars per thousand with fry liberations and 200 dollars per thousand with fingerling liberations. This would not only decrease cost of liberations but increase output in those hatcheries now rearing yearlings. In this way it would be possible to stock the lake with a larger number of trout in order to increase production to accommodate increased angling and improve angling success.

It seems that as a result of the relationship of trout and shiners in Paul Lake it would seem advantageous to attempt the removal of shiners from this lake. The cost of removal is now at a lower level than previously and while yearling liberations have been an extremely successful stop-gap technique it appears greater production of trout is possible in a lake free of shiners. The size of the body of water involved and characteristics of the redside shiner make total eradication of shiners doubtful. It is the opinion of fishery biologists in other areas of north-west North America, where similar problems have arisen, that even partial kill of coarse fish leads to large increases in production of trout. This is required to meet the rising demand on sport-fishing lakes as a result of increasing population.

When trout are the prime consideration, lake ecology must be manipulated with the idea of increasing the production of this species even though trout and some other fish, intermediate in the food chain, might be a more efficient utilization of food resources of the lake. The Paul Lake study indicates the necessity of eradication of shiners in this lake in order to accomplish maximum production of the desired species. The study also points out that factors involved in the interaction of predator and prey are complex, changing and so subject to variability that it is obvious that each predator-prey situation is possibly a unique biological phenomenon requiring investigation previous to any management decision.

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