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THE SUMMER MIGRATION OF THE CISCO, *LEUCICHTHYS ARTEDI* (LE SUEUR), IN LAKE NIPISSING, ONTARIO

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THE SUMMER MIGRATION OF THE CISCO, *LEUCICHTHYS ARTEDI* (LE SUEUR), IN LAKE NIPISSING, ONTARIO

Abstract

In lake Nipissing there is a general migration of the cisco population from shallow to deeper water in late spring and early summer which takes the fish participating in it below the thermocline. The fish remain in the hypolimnion for some time, scattering downwards. During late August and early September they rise from the bottom and concentrate under the thermocline. Most of them pass through the thermocline and return to shallower water before the autumn turnover.

The downward movement is correlated with rising temperatures in the epilimnion until the fish have passed through the thermocline. Their continued descent is probably due to random dispersion. The subsequent ascent from the bottom is correlated with a depletion of the dissolved oxygen and an increase in the carbon dioxide in solution in the bottom water. This ascent from the bottom results in a concentration of the population immediately under the thermocline. The population ultimately moves upward when the balance between the opposing effects of high epilimnial temperatures above and unfavourable concentrations of dissolved gases below is destroyed by the continued cooling of the epilimnion and further stagnation in the hypolimnion.

An orderly succession of certain groups of individuals is apparent in the migration. The largest males migrate downward earliest. These are followed by the largest females and by large males and so on. The two youngest age classes are the last to move downwards and their migration is never so complete as that of the older groups. The pattern of the upward movement is more complicated. Quite large but by no means the largest fish pierce the thermocline earliest; the order of leaving subsequent to this involves fish both above and below the intermediate sized group which left first. The smallest fish leave late and the last of all to go are the largest males. This order of migration has been explained as being the result of a decrease with age of tolerance towards the factors initiating migration.

Profound changes in feeding activity are correlated with the summer migration. The ciscoes apparently stop feeding just prior to migrating below the thermocline and may not begin feeding again for six weeks or longer. The length of time during which they do not feed varies with the time at which they migrate. When the fish leave the hypolimnion in late summer they again stop feeding for an undetermined length of time.

The migratory and feeding activities of the individual are related to its rate of growth. Certain individuals found to be feeding in the hypolimnion in July grow more quickly than fish of the same age and sex which are not feeding there at that time. The proportion of the members of a year class which feed in the hypolimnion in July increases as the year class becomes older. Correlated with this increase in feeding activity there is a general acceleration of growth in the higher age groups.

Introduction

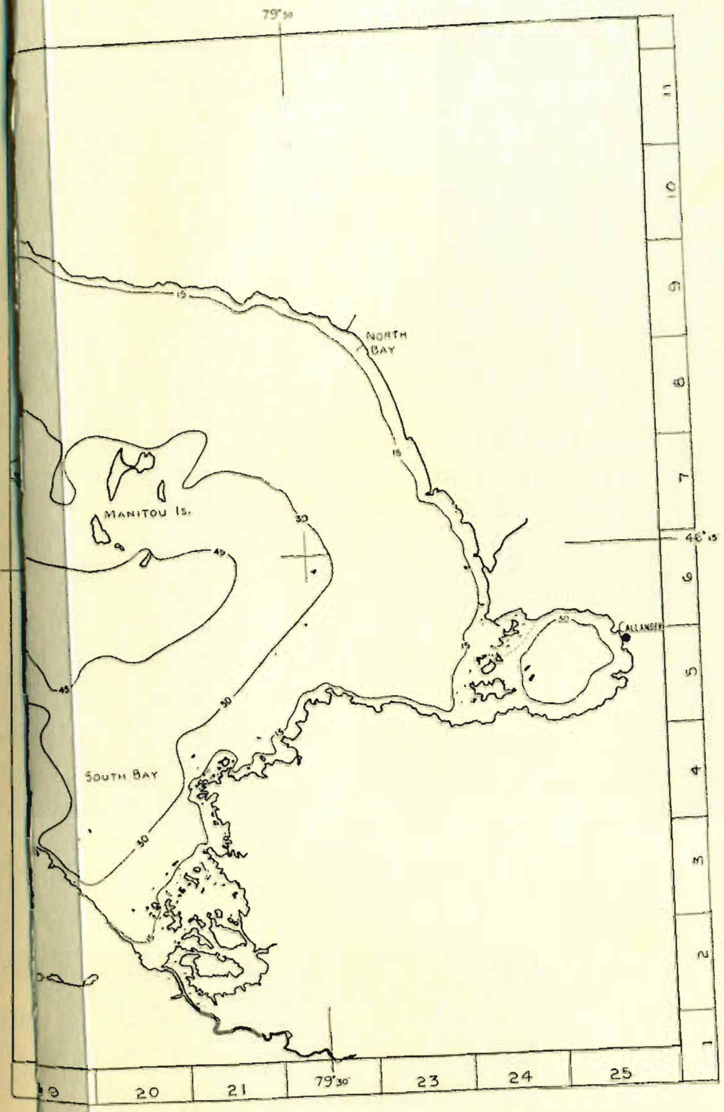
The cisco, *Leucichthys artedi* (Le Sueur), has been the subject of much investigation. Studies on its rate of growth and other phases of its life-history have been contributed by numerous authors, and its variation in form has also received considerable attention. The great gap in our present knowledge of this species lies in the lack of precise information of its habits, and the relation that these habits bear both to the great variation in growth rate of this species in different lakes, and to its proverbial diversity of form.

During the years 1929 to 1935 inclusive, when the Ontario Fisheries Research Laboratory, of the University of Toronto, had a field station on lake Nipissing, an opportunity was afforded for some work on the variation and on the movements and feeding activities of the cisco. Our attention was not directed towards a study of the migration until after a considerable amount of preliminary work had been done. When Professor J. R. Dymond first visited the station in 1930, he was struck by the great variation in form exhibited by the ciscoes in lake Nipissing. It seemed to him that this circumstance might afford a suitable opportunity for an investigation which might provide some insight into the problem of raciation in this species.

During the first two seasons, ciscoes, taken in routine net settings which were being carried on as part of a general ichthyological survey of the lake, were selected without reference to their systematic characters. Professor Dymond measured various characters of these fish, commonly considered of taxonomic importance. It was found that there was a wide variation in the proportions of certain parts. For instance, the relative length of the head covered 65 per cent. of the total range of this character found by Koelz (1931) in the type races of the twenty-four subspecies recognized by him. On this basis one would expect to find at least two or three subspecies in lake Nipissing.

However, in a preliminary study of the taxonomic material, no facile interpretation presented itself. Although the total range of variation was great the distribution was, on the whole, unimodal. Further, no consistent differences could be detected between samples from different localities, nor could samples from one locality be relied on to exhibit consistently the characters of one particular section of the total range of variation.

From these findings it was concluded that study of the



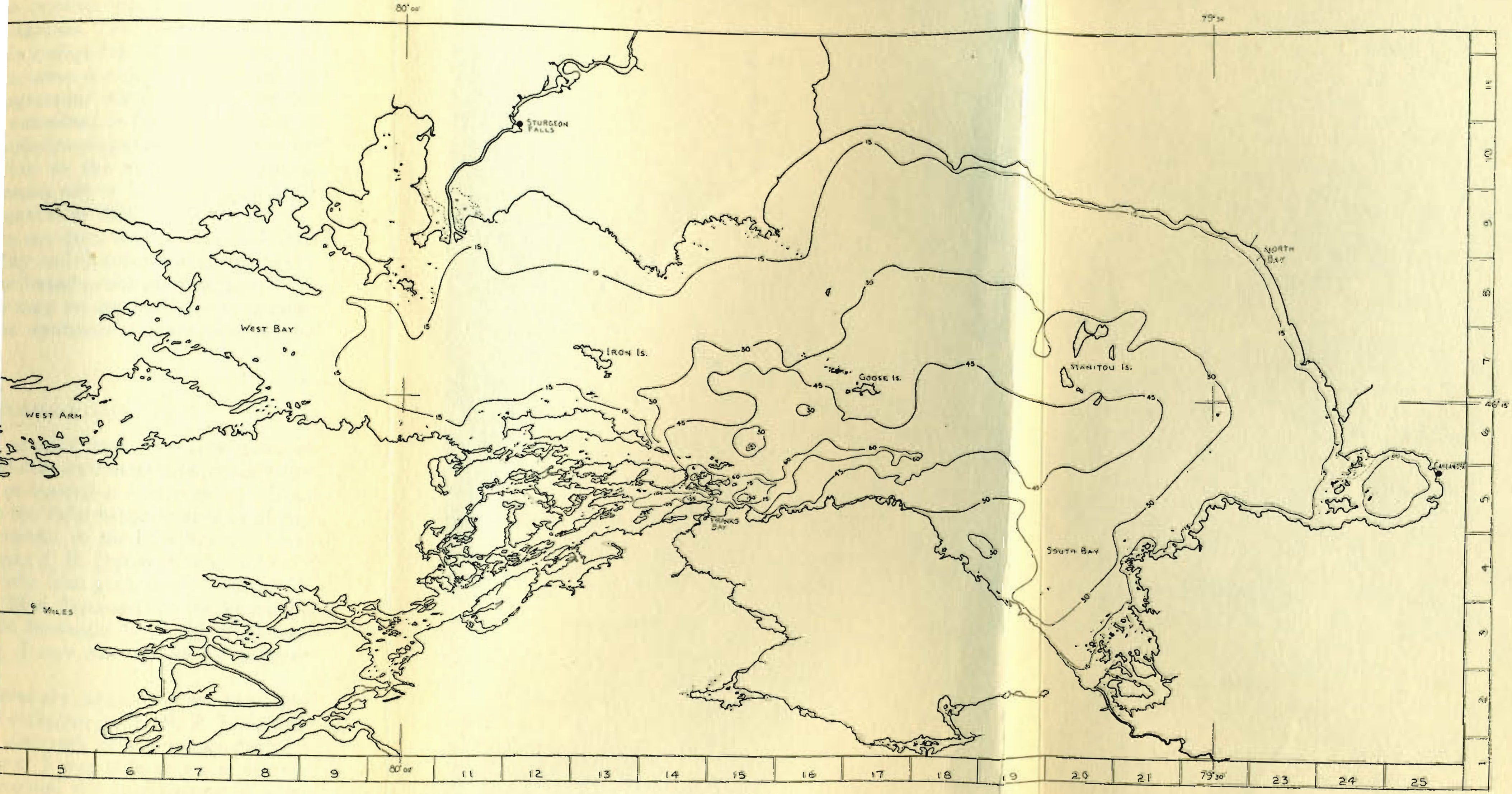


FIGURE 1.—Map of lake Nipissing showing depth contours at 15 foot intervals.

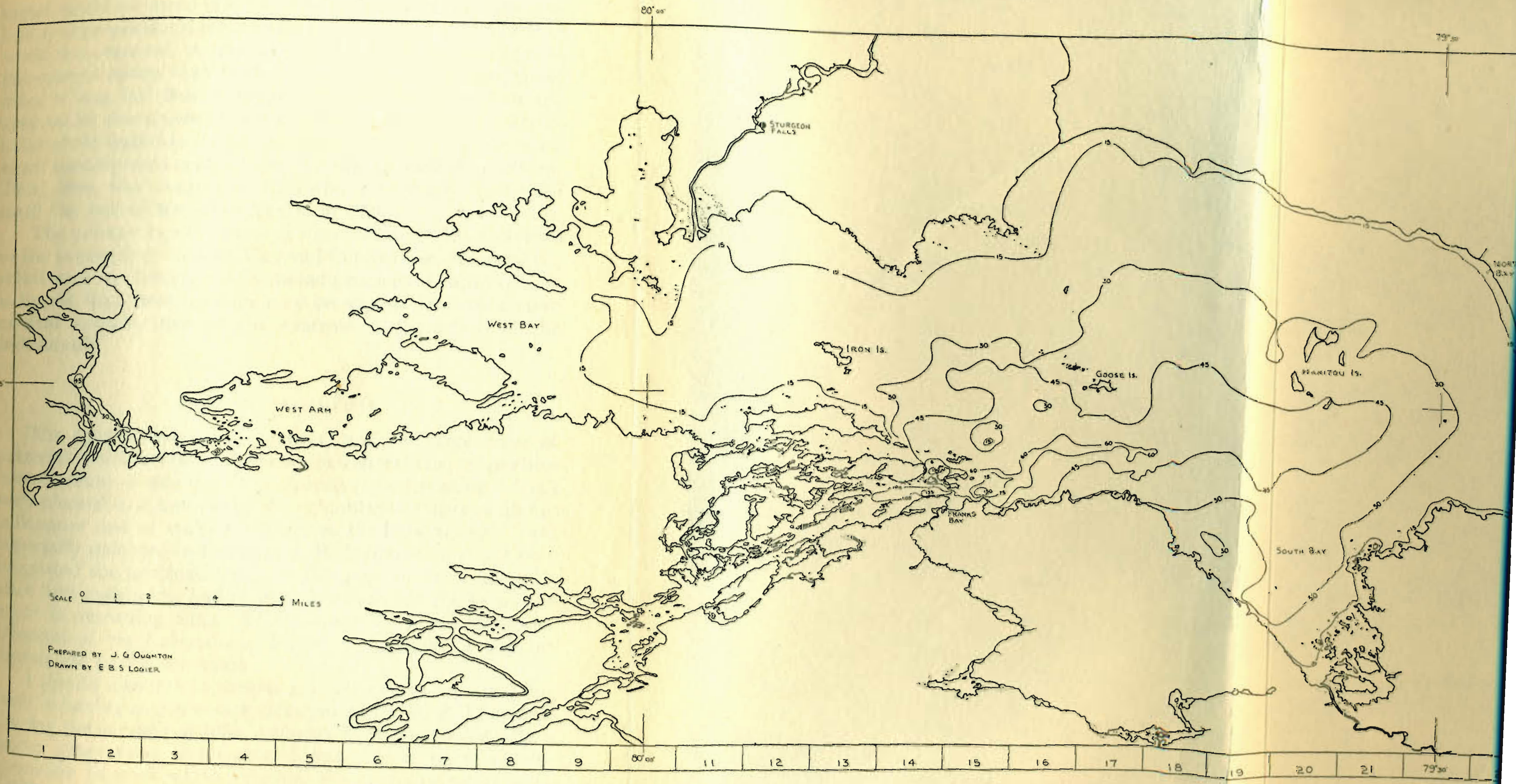


FIGURE 1.—Map of lake Nipissing showing depth contours at 15 foot intervals.

racial problem could not be centred solely on the accumulation of proportional measurements. For this reason further work was devoted to the investigation of the ecology of the species rather than to the mere acquisition of specimens, since it was felt that a programme which would allow the systematic characters to be examined in the light of a knowledge of the habits of the population would be likely to yield a more fundamental contribution to the taxonomic problem. This, then, was made our main object of study from 1932 until the end of the investigation in 1935.

The present report covers our knowledge of the activities of the population between May and October and discusses the relation of our findings to the broad problem of raciation. It is hoped that these findings may be applied later to a more critical consideration of the systematic characters of the individuals.

ACKNOWLEDGEMENTS

The considerable array of gear, and the large mass of material that must be worked over in a short time, render any investigation of this type a co-operative undertaking. I am very pleased to acknowledge the valuable assistance of all my colleagues and of various visitors to the Laboratory. I am especially indebted to Professor J. R. Dymond, who not only suggested the problem, but who also gave freely of his guidance and assistance, and to Mrs. Dymond for the hours she spent in recording data. To Professor W. J. K. Harkness, Director of the Laboratory, I owe my thanks for support during the past seven years.

I should also like to express my pleasure in my good fortune in having so generous a colleague as Dr. R. R. Langford. During the summer of 1935, although he was occupied with a heavy programme of his own, I was able to enlist his cooperation in work which involved the examination of some 6,000 fish.

The physical chemical data presented here are largely the result of investigations by Dr. G. H. W. Lucas and Dr.

J. M. B. Corkill, and have been taken in part from their original records, and in part from Dr. Corkill's manuscript report.

Finally, I should like to acknowledge my indebtedness to Dr. R. O. Hile and Dr. John VanOosten of the United States Bureau of Fisheries, who have been kind enough to give the manuscript a very thorough and constructive criticism.

DESCRIPTION OF LAKE NIPISSING

Morphometry

Lake Nipissing lies in the Precambrian shield, lat. 46 N. long. 79 W., at an elevation of 640 feet. The lake has an area of 345 square miles. In shape it is long and narrow; the long axis extends east and west for some 50 miles while it is on the average less than 12 miles wide. Lake Nipissing is rather shallow, the western half being almost uniformly less than 15 feet deep. The accompanying map (figure 1) shows the depth contours in intervals of 15 feet, and the proportions of different depth zones are given in table 1. It will be noted that only about one-half of one per cent. of the lake is over 75 feet deep. This deep water is all found in the vicinity of the source of the French river ([15, 5], figure 1).[1]

TABLE 1.—Percentage of the area of lake Nipissing below certain depths.

Percentage	Depth
100	0
68	15
12	45
2	60
0.5	75
0.3	105
0.1	150

Temperature Conditions

Temperature records for a number of years are shown in figure 8 (p. 29). The ice leaves the lake in late April or

[1]The co-ordinates given on the map should be noted since these will be referred to throughout this paper in locating stations and in designating specific localities thus—([15, 5], figure 1), the abscissa being given first.

early May. Thermal stratification begins in May, is well established by the end of June, and persists until October. The bottom temperature in summer varied between 8 and 10°C. during the years that observations were made. The maximum surface temperature was about 24°C.

Oxygen Depletion in the Hypolimnion

During the period of thermal stratification the oxygen depletion in the hypolimnion is marked, and at the bottom

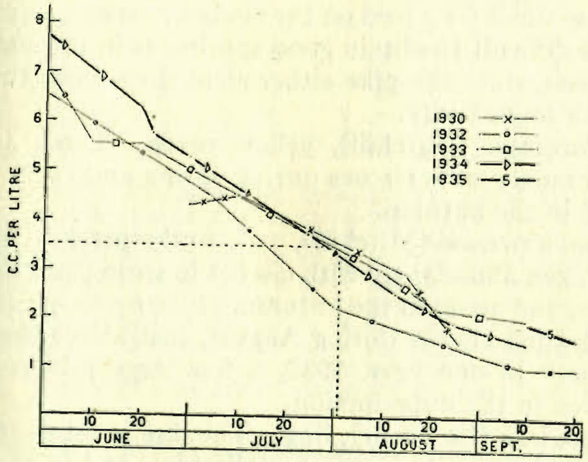


FIGURE 2.—Oxygen depletion at 150 feet during the summers of the years 1930-1935 inclusive. After Corkill.

(150 feet) the dissolved oxygen drops to between one and two cc./1. in September (figure 2). Coupled with the decrease in oxygen is an increase in carbon dioxide which reaches concentrations higher than 15 parts per million.

Fishes Associated with the Cisco in Lake Nipissing

The following is an annotated list of some of the species of fish taken in the gill nets during the course of collecting the ciscoes.

Acipenser fulvescens Rafinesque, sturgeon. The sturgeon has been taken with ciscoes in early spring and late fall.

Coregonus clupeaformis (Mitchill), common whitefish. In summer the whitefish occurs in association with the cisco in moderate depths, occasionally found in the hypolimnion.

Catostomus commersonii (Lacépède), common sucker. The sucker is also associated with the cisco in shallow water in spring, early summer, and autumn.

Esox lucius Linn., pike. Pike are taken along with ciscoes in the same seasons as are the perch and the pike-perch. At these times they feed on the ciscoes to such an extent that it is difficult to obtain good specimens in the smaller size classes, since the pike either steal them from the nets or slash them badly.

Perca flavescens (Mitchill), yellow perch. Perch are found commonly with ciscoes during spring and early summer, and in the autumn.

Stizostedion vitreum (Mitchill), yellow pike-perch. This species is taken abundantly with ciscoes in spring and early summer, and again in the autumn. Large pike-perch feed on fingerling ciscoes during August, just above the thermocline. In one year, 1932, a few large pike-perch were taken in the hypolimnion.

Lota maculosa (Le Sueur), ling. The ling is taken frequently with the ciscoes in the hypolimnion and in the shallow water in early spring. The cisco forms a considerable portion of the summer food of the ling.

This does not exhaust the list of species found in lake Nipissing. It is given merely to provide some idea of the fish associated with the cisco in this lake.

MATERIAL AND METHODS

Description of the Cisco Found in Lake Nipissing

A summary of certain systematic characters of the lake Nipissing cisco is given in table 2. These measurements were made by Professor J. R. Dymond and have been compared

with his measurements of the ciscoes of lake Nipigon (Dymond, 1926), lake Abitibi (Dymond and Hart, 1927), and western Canada (Dymond and Pritchard, 1930). They have also been compared with Pritchard's (1931) measurements for lake Ontario and with those of Koelz (1929, 1931), of the ciscoes of the great lakes, and of other lakes of north-eastern America.

TABLE 2.—Summary of certain characters of lake Nipissing ciscoes, expressed in thousandths of the standard length.

No. of fish	Average length in mm.	Scales	Gill rakers	Head length	Head depth	Eye	Snout	Body depth	Body width	Caudal peduncle Length	Caudal peduncle Depth	Dorsal height	Anal height	Pectoral length
Males														
10	195	70	19 & 34	239	160	62	60	276	143	120	96	177	112	168
10	209	70	19 & 34	239	158	61	60	275	142	114	94	174	114	167
10	219	68	19 & 34	242	162	62	62	277	144	114	95	175	113	172
10	228	69	19 & 33	242	162	63	62	290	139	113	95	180	118	173
10	236	72	19 & 34	241	162	60	61	288	144	117	95	176	116	174
10	244	..	18 & 33	242	160	60	60	286	139	111	94	182	118	174
10	259	67	19 & 34	245	164	61	62	302	145	116	95	176	120	178
10	284	67	19 & 35	246	165	60	64	283	137	114	94	185	127	188
10	315	71	19 & 35	238	163	55	62	269	147	113	91	167	114	173
9	392	74	20 & 36	238	167	48	66	276	143	118	87	157	110	168
Females														
10	204	69	18 & 32	244	164	63	61	285	146	119	97	179	118	174
10	220	70	19 & 34	246	163	62	59	275	146	118	94	177	116	168
10	229	70	19 & 35	234	162	62	61	288	160	124	94	178	120	173
10	237	70	18 & 35	238	157	60	61	290	147	114	96	178	115	170
10	245	69	19 & 34	234	157	59	59	279	142	116	92	178	115	169
10	253	69	19 & 34	246	166	62	62	293	144	114	96	178	134	175
10	266	68	19 & 35	240	159	60	60	285	141	124	95	183	120	174
10	294	70	19 & 34	240	164	58	61	282	138	116	94	165	117	173
10	348	70	19 & 35	241	166	50	65	281	141	120	90	166	112	169

Of the subspecies of *L. artedi*, the Nipissing ciscoes compare most closely with *L. artedi wagneri* which Koelz (1931) has described from Tomahawk lake, Wisconsin, but the Nipissing fish grow faster and reach a much larger size. The Nipissing ciscoes also resemble strongly the species *Leucichthys nipigon* Koelz (*cf.* Dymond, 1926), differing most in having a lower gill raker count. Despite this similarity we prefer not to identify the Nipissing ciscoes with *L. nipigon* for the present. In view of the resemblance of the Nipissing fish to both *L. artedi wagneri* and *L. nipigon*, it is felt that the problem of the relationship of the species *artedi* and *nipigon* is still an open question.

The variation of the characters of *artedi* from lake to lake is so great as to render it impossible at present to make satisfactory infraspecific identifications. For this reason we prefer to describe the Nipissing form without naming it, hoping that this description, together with an outline of its ecology, will allow some future worker to assign it to its proper taxonomic position.

Method of Sampling

This study was carried out by exploring the lake with some 200 gill net settings. The mesh of the gill nets ranged in size from about ¾ to 5 inches stretched mesh. The smallest mesh was made of milliner's net ordinarily used in trimming women's hats. This net was used successfully in taking fingerling ciscoes. Hung between two 1½ inch meshed gill nets for protection, it proved to be quite durable and was fished for three seasons.

The nets were set in various ways—on bottom in the conventional manner, floated at the surface between two buoys, floated at some point intermediate between bottom and surface, or set obliquely from bottom to surface. When setting on bottom it was customary to use a series of 50 yard nets with mesh ranging from 1½ to 5 inches. The surface and intermediate sets consisted of only one 50 yard net. In the oblique sets each stratum was fished once by a small, an intermediate, and a large meshed net. Table 3 gives particulars of the two series most commonly used in bottom fishing. Details of the oblique series are given in appendix 1.

TABLE 3.—Yardage of nets used in standard strings set on bottom.

	Stretched mesh in inches									
	1½	2	2¼	2½	2¾	3	3½	4	4½	5
String 1	50	50	50	50	50	50	50	50	50	50
String 2	50	..	50	50	50	..	..	50	..	..

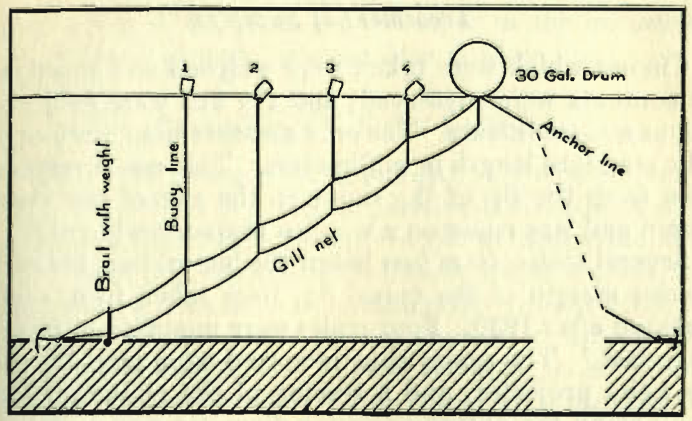


FIGURE 3.—Diagram showing method of setting nets obliquely.

Localities Sampled

The accompanying chart shows in black the localities where fishing was carried on. Sampling was done most intensively at stations selected to cover the range in depth found in the lake. Where the bottom was uniform over great distances, a few widely-spaced samples were taken to determine to what extent the samples at a single station were representative of the total zone.

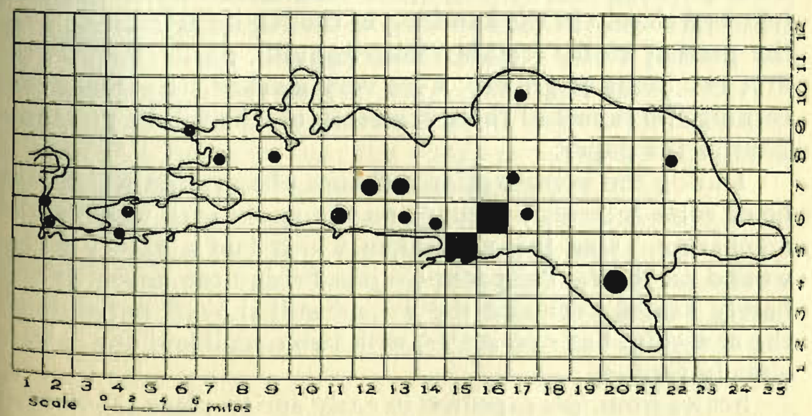


FIGURE 4.—Diagram showing localities sampled by net settings.

Treatment of Samples

Ciscoes which were taken were weighed and sexed; stomach contents were preserved; and the fish were subjected to various measurements. The only measurement discussed here is the standard length in millimetres. This measurement was taken from the tip of the snout to the end of the vertebral column and was made on a wooden measuring board.

Several scales, from just below the lateral line, beneath the anterior margin of the dorsal fin, were taken from each fish measured after 1930. Four scales were mounted in glycerine-waterglass.[2] The scales thus mounted were read by the use of a Leitz projector, and a tracing of the boundaries of the annuli along the antero-posterior diameter was preserved on a filing card. The glycerine-waterglass mount has optical properties that are superior to those of glycerine-gelatine but the mount is not permanent. The medium crystallizes with age and becomes opaque, first at the edges, and progressively towards the centre of the mount. In mounts three years old considerable encroachment has already taken place.

Scale Reading

There is little that the present writer can add to Van-Oosten's work on the reading of cisco scales, which has been followed closely in the handling of the Nipissing material. In the present study certain "false annuli", particularly in the first two years of growth, were very marked. Evidence concerning the causes of these accessory checks will be presented later in the paper.

During the investigation a chance observation which may be of some interest was made on the speed with which scales regenerate. One fish was taken which had a rather severe wound on the caudal peduncle just behind the anus. It was barely healed over and the wound still showed red through the new skin, but new scales, with two circuli laid down, were already formed.

Scales from fish captured in early spring place the date of

[2]Six volumes of waterglass to one volume of glycerine.

the completion of the annulus, or rather of the initiation of the new season's growth, at some time in May.

The Reliability of Gill Net Catches

Much of the subsequent argument is based on the assumption that there is a strong positive correlation between the numbers of fish taken by a given gill net fished for a fixed period of time, and the concentration of fish in a given locality. There would seem to be considerable evidence that such a correlation exists. Data on the number of fish taken by fishing equivalent amounts of net in the same locality, simultaneously, or on consecutive nights (table 4), show that there is a fairly good agreement between the pairs of settings.

TABLE 4.—Number of ciscoes taken in comparable fishing effort under similar circumstances.

Set 1	Set 2
22	24
25	26
105	60
64	49

Evidence such as is given in table 4, while indicating that the net catches bear some relationship to the number of fish in a given locality at a certain time, does not show that the fish themselves are distributed randomly throughout a given stratum, either as individuals, or in small freely wandering schools. However, the surface catches, where a net left out for long periods was cleared daily, show that in one locality there is a definite trend in the number taken, which is consistent with the belief that the numbers taken are not due to erratic movements of large schools (figure 9, p. 30).

The results of the oblique series, by their consistency, also indicate both that numbers taken are proportional to the numbers present, and that the population exhibits a definite movement. Since different meshes were fished in different strata on the three nights of the series, a certain amount of interest was taken in plotting the results of the first two nights for a given mesh, and predicting the third night's catch from these. The predictions were reasonably accurate.

The correlation between catch and population need not necessarily be a linear one, and in all likelihood it is not. Gill net fishing, which requires the fish to come in contact with the net, must depend on the activity of the fish. This activity may vary because of many factors. The analysis of stomach contents (Langford, 1938) shows, for example, that when food is scarce the fish apparently are more active in seeking it. This condition would probably increase the number of fish taken, relative to the number present. Temperature probably also influences activity, but no evidence of this is available. Further, fish apparently avoid gill nets under certain circumstances. The following example (table 5) shows that they may do so in daylight.

In the daytime no small fish were taken. Medium and large fish were taken in the bottom stratum in numbers comparable to those taken at night. In the 15 to 20 foot stratum a few medium and large fish were taken and a single large fish was taken at the surface. This evidence would indicate, unless of course fish leave the locality in the daytime, that the fish avoid the nets in water down to 30 feet in the light, and even below this depth if the mesh is close, as it is in a 1½ inch mesh.

TABLE 5.—Relation of light to the capture of ciscoes by gill nets.

Depth	Number taken of the lengths indicated			
Feet	20 cm. and less	20-25 cm.	25 cm. and greater	
0-15..........	2	34	20	night
	0	0	1	day
15-30..........	7	32	12	night
	0	6	1	day
30-bottom......	4	28	16	night
	0	19	15	day

Again when some fish are enmeshed others may avoid the net. Hile (1935) has shown that in commercial fishing, much higher returns can be obtained from clearing nets at short intervals of time. Here, however, this factor has been neglected in comparing catches where the time for which the nets were fishing differs. In these cases a simple ratio based

on the length of the fishing period has been employed to correct the inequality.[3]

Due to the selectivity of gill nets (for a review of the literature and data on *L. artedi* see Hile, 1936; see also Tester, 1935), changes in size composition also affect the relative number of fish taken by a standard graded series of gill nets due to the difference in the efficiency of each net for each size class. The effect of size composition has also been disregarded in the present discussion because of its complexity.

VERTICAL DISTRIBUTION FROM MAY TO OCTOBER

Introduction

In 1934 and 1935 the summer movements of the cisco population were followed in some detail. This migration consists of a progressive movement of the population from shallower to deeper water during the months of May, June, and July. In August most of the ciscoes are concentrated in the restricted hypolimnion. In late summer they pass upward through the thermocline and reappear in shallow water.

1934 Catches

In 1934 settings were made from the beginning of May when the lake was still largely covered with ice, until the middle of September. In this fishing, bottom, surface, or intermediate, nets (see p. 16) were set at the stations whose positions are plotted on the accompanying maps (figures 5 and 6). These stations were considered to be representative of the range of depths found in the lake except for the large area of shallow water at the western end which is less than 15 feet deep.

STATION 1.—The channel at the head of the French river. A setting in about 75 feet of water was made here on May 2; this location was chosen mainly because it was part of the small area free of ice at that time.

STATION 2.—About a quarter of a mile to the north and east of station 1, just south of the eastern Blueberry island, is an area of water about 45 feet deep. The bottom here is somewhat of the nature of a triangular terrace rising to the islands on the north and sloping steeply to the deep water on the other sides.

[3] Hile (personal communication) states: "We have found that abundance curves computed without any reference to fishing time are fully reliable, and are far superior to curves computed from the 'catch per net per night'."

STATION 3.—About half way between the Blueberry and Goose islands, this station was chosen as being typical of the open water of the main lake; the depth here is about 45 feet.

STATION 4.—This is a rather restricted area of water, one of the three known "deep holes", 150 feet deep, just where the open lake joins the source of the French river.

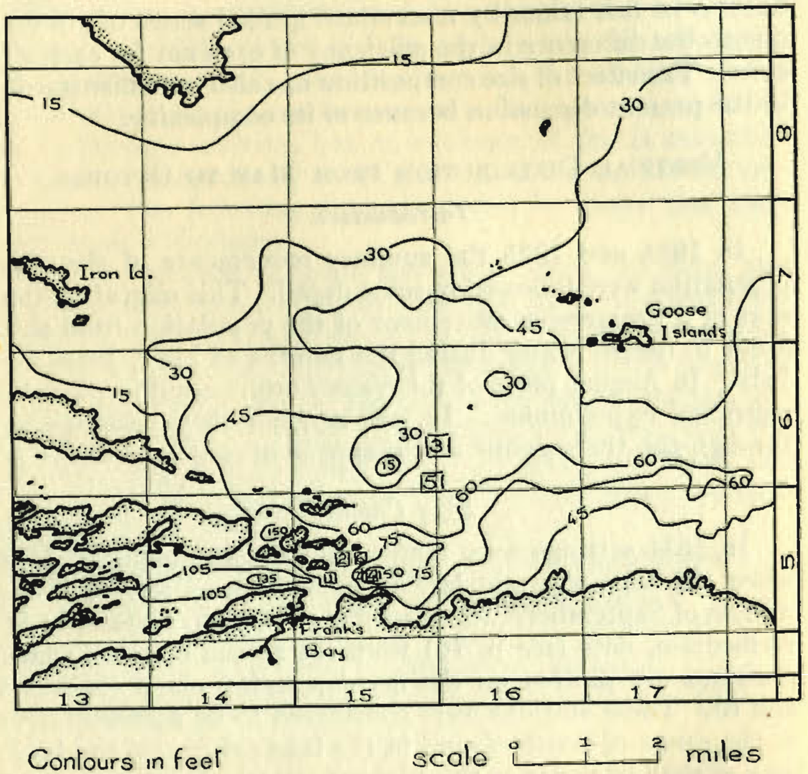


FIGURE 5.—Map of the area of lake Nipissing fished in 1934.

STATION 5.—When the catch fell off at station 3, a net was set about one-third of the way from that place towards station 4 to make certain that the fish had left the shallow water.

STATION 6.—East of the Blueberry islands just at the edge of the deep water where the bottom slopes suddenly from 45 to 90 feet.

STATION 7.—Just south of station 2 and west of station 4, in water 90 to 100 feet deep. This location was chosen because of its proximity to the thermocline which at that time was between 105 and 115 feet.

TABLE 6.—Vertical distribution of ciscoes taken in 1934.

Depth in feet	May	June	July	August	September
0–15					
15–30					
30–45	May 4 7 May 5 6 May 15-17 64	June 23 100	July 16 154 July 24 29	Aug. 3 10 Aug. 29 7	Sep. 3 22 Sep. 4 10 Sep. 7 24 Sep. 8 6 Sep. 14 8
45–60				Aug. 4 19 Aug. 7 8	
60–75	May 3 4			Aug. 30 25	
75–90					
90–105					Sep. 12 20 Sep. 15 41
105–120					Thermocline
120–135					Sep. 11 650
135–150	May 10 1	June 3 2		Aug. 16 377	Sep. 10 110 Sep. 16 46

The 1934 catches are recorded in table 6. It may be seen that just after the break-up of the ice very few ciscoes were taken in any one catch. In late May and early June the catch in 45 foot water increased, while there were still but few fish caught in the very deep water. This concentration at 45 feet continued to increase until a peak was reached during the middle of July. After this time there was a rapid falling off in the number caught at this depth, and an increase in the

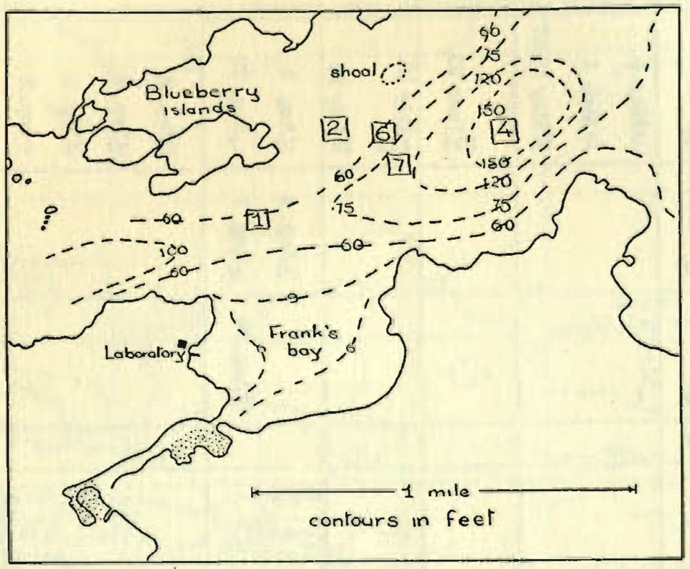


FIGURE 6.—Sketch map of the region at the head of the French river.

number taken in the cold water below the thermocline. The fish remained in the hypolimnion throughout August and into the beginning of September. During September the catches in shallow water increased slightly, this increase continuing and becoming most marked in the last catch, taken on September 15 just above the thermocline.

The deep water catches in September show a very striking stratification of fish. A net set on the bottom on September 10 in 150 feet, gave a catch equivalent to 110 fish in string II. This number is about half that which was taken at the same place in the middle of August, in spite of the fact that the thermocline had descended from 75 to 105 feet, thus decreasing

the volume of the hypolimnion. At the same time the catches in shallow water had not increased greatly and consequently one would have expected a great increase in the number taken in the hypolimnion. However, the same net set 18 feet from the bottom on the following night, directly above the position of the previous night's setting, caught the equivalent of 650 fish. This great concentration was confined to the upper waters of the hypolimnion, for on the night of September 12, the net was set on bottom in a depth of from 90 to 100 feet, which was just above the thermocline, the locality being sounded and buoyed so that the position of the net could be determined rather precisely. In this location, just a few hundred yards west of the position of the previous settings in the hypolimnion, the equivalent of only 20 fish was taken.[4]

1935 Catches

It has been pointed out that the 1934 series lacked samples from water less than 45 feet deep. It was inferred that the increase in the number of fish taken at 45 feet during June and July resulted from the evacuation of the area of shallower water. In May, 1935, considerable numbers of fish were taken in West bay ([11, 6] and [12, 7], figure 1, opposite p. 10) where the water is only 15 feet deep. In this and other localities where the water is the same in depth, a cisco is a rarity in August.

By the end of May, 1935, considerable information about the extent and nature of the movements of the population had been obtained, but it was largely limited to the interpretation of the results from gill nets set on the bottom. True, a considerable number of surface sets had been made, and also occasionally a net had been floated up from the bottom to an

[4]In these catches only one 50 yard net of 2¾ inch mesh was used, and to calculate the equivalent to string II the number of fish captured was compared to the same number caught in the same net in the catch of string II made under conditions most closely approximating those under which the net in question was set. The figure for the population has been taken as that proportion of the total catch of string II as is represented by the ratio

$$\frac{\text{catch of net set}}{\text{catch of the same net in string II}}$$

"intermediate" position, but the laboriousness of these methods made impossible an extensive vertical sampling of the water over any one locality. In June, 1935, the problem was attacked by the use of "oblique" nets (see p. 17). A set of this type allows a vertical sample to be taken of the fish at a given locality. Series of this nature were taken at two stations, a shallow water series at station 3, and a deep water series at

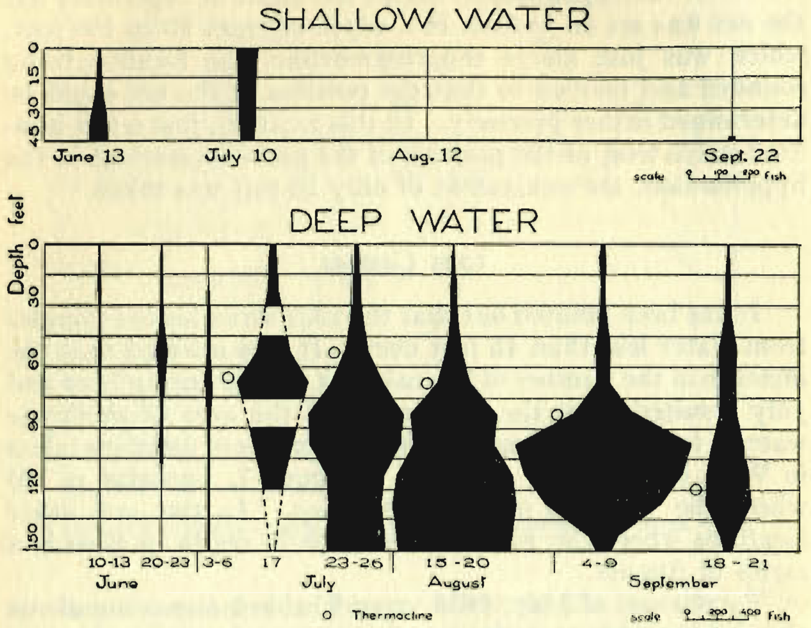


FIGURE 7.—Vertical distribution of ciscoes taken in oblique series in 1935.

station 4 (p. 22). The results of this fishing are given in tables 7 and 8, appendix 1, and are illustrated in the accompanying graph (figure 7).

Since station 3 had been sampled fairly intensively in 1934, only three series were carried out here on critical dates. An early sample was taken on June 13, in which the fish were found to be concentrated in the lower fifteen feet. The next series shows quite a different picture of vertical distribution.

On this date, July 10, the fish taken were distributed almost uniformly from the surface to the bottom. At this time the mayflies were emerging and the fish were feeding largely upon these at the surface. This surface feeding apparently influences their distribution. In the August 12 series no ciscoes were taken in the shallow water. For the sake of completeness, the result of a bottom set lifted on September 22, is also shown in figure 7. On this date six fish were taken in 50 yards of 2¼ inch mesh.

The collections resulting from deep water sampling at station 4, consisting of seven complete series and one partial one, give a more complete picture.

The first fishing was done here between June 10 and 13. At this time there were few fish in this vicinity and practically all of these were taken at depths of less than 75 feet. By June 20 there had been some increase in the population, principally between 45 and 60 feet, and some fish were taken in the deeper strata. The next series, taken July 3 to 6, showed no gain in the numbers of fish taken, but there had been a further downward shift in the population.

Between the sixth and the seventeenth of July there was a great influx of fish to the vicinity of station 4. The number taken on July 17 was so great that the setting of the series of nets could not be completed. While there were more fish taken in every stratum, the greatest increase was at depths of between 60 and 75 feet. A week later, July 23, fishing was resumed with shorter yardage of net and there was a further increase in the relative number of fish captured. At this time most fish were taken at depths of between 75 and 105 feet. From 105 to 150 feet the fish were almost uniformly distributed but in much greater numbers than before. The August 15 to 20 series shows a still further downward movement of the population. More fish were taken over this period than in the previous series, but this increase is probably due to a greater concentration of the fish already below the thermocline, in the lesser volumes of the bottom strata, rather than to a further ingress of fish from shallow water.

The first series in September, taken from September 4 to 9, shows an upward shift of the population which has resulted in a distribution comparable to that found on September 10, 11, and 12, 1934 (pp. 24-5). The last series of the year was taken over the period from September 18 to 21. By this time the catch had decreased considerably in the lower strata and increased in the upper layers, indicating that the migration from the hypolimnion was at this time well under way.

CAUSAL AGENTS OF THE SUMMER MIGRATION

At no time during the six seasons were large numbers of ciscoes taken in water that had been long above 20°C. This may be seen by reference to figure 8 which summarizes the results of bottom fishing from 1929 to 1935. Twice during that period large catches were taken in water at about 20°C. (July 25, 1930, and July 16, 1934), but in these instances that temperature had just been reached. Further, in 1934 and 1935, when the movements were followed more closely, it was found that the fish left the shallow water quite suddenly after the temperature rose to 20°C. Within a week, the catch dropped off from 154 to 29 per unit effort, during 1934, and in 1935 the population moved into deep water with a similar suddenness. The catches taken by oblique series are not shown in figure 8; for these data, figure 7 must be consulted.

Evasion of water above this apparently critical temperature will not completely explain all movements from shallow to deeper water. It would seem likely that, when temperature conditions are not unfavourable, the presence of the ciscoes at the surface is influenced by the abundance of mayfly emergents on which they gorge themselves during June and July. The effect of mayflies on the vertical movement of ciscoes is strongly indicated by the nature of the catch of July 10, 1935, where the mode of distribution was at the surface at a time when the mayflies were emerging (figure 7).

A further instance of the effects of mayfly emergence is seen in the surface series taken in 1932 and 1933. These two series represent contrasting conditions in the surface temperature and with it the temperature of the upper strata in gen-

eral. The numbers taken in these series are shown in figure 9. On the same figure are plotted the temperatures at the surface and at a depth of 30 feet. The 30 foot temperature is given as perhaps a better indication of any upper limit to temperature

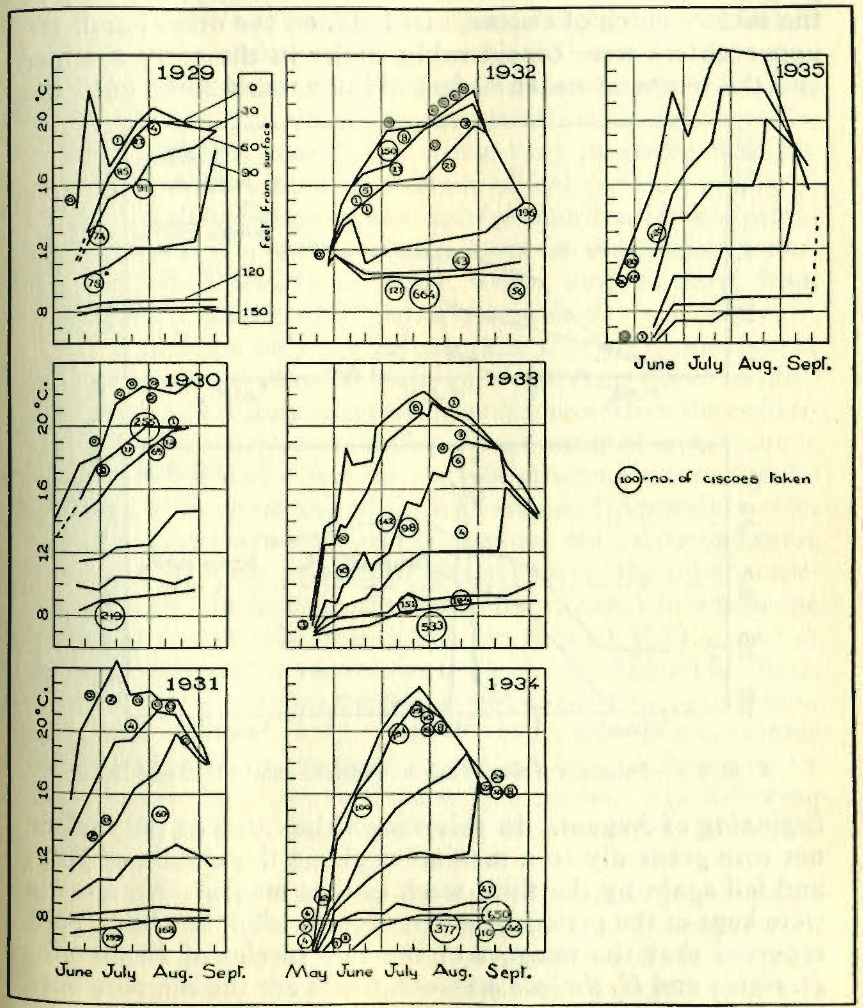


FIGURE 8.—Numbers of ciscoes taken in gill nets plotted in relation to season, depth, and temperature. Temperatures from Corkill.

conditions affecting the presence of the ciscoes in the surface nets, since the fish are not necessarily limited in their movements to the immediate surface layer.

In 1933 the temperature at 30 feet reached 20°C. about July 10, and at this time there was also a precipitous drop in the surface catch of ciscoes. In 1932, on the other hand, the upper waters were considerably cooler in the early summer and the temperature at 30 feet did not reach 20°C. until the

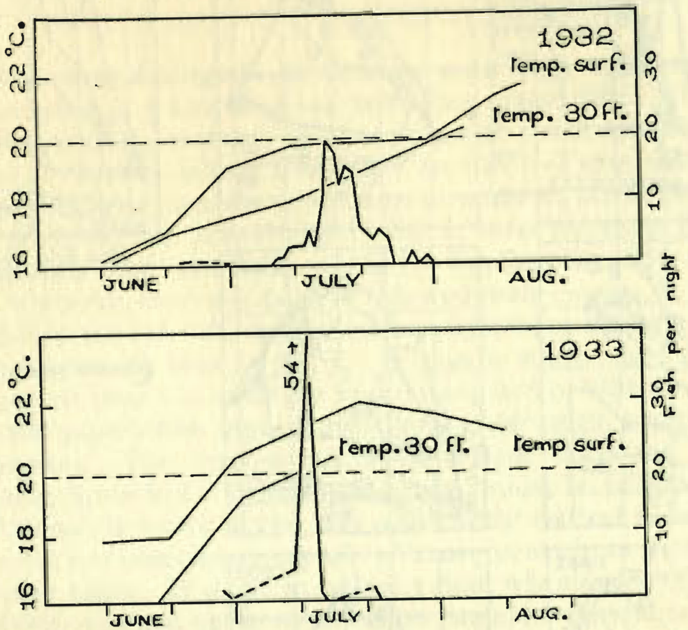


FIGURE 9.—Numbers of ciscoes taken in surface nets in 1932 and 1933.

beginning of August. In this season the catch of the surface net rose gradually to a maximum about the middle of July, and fell again by the third week of that month. No records were kept of the period of emergence in 1932, but Ide (1930) reported that the imagoes of the two species of *Hexagenia*, *H. rigida* and *H. limbata occulata*, which are the common ones in lake Nipissing, emerged from July 6 to 25 in 1929, in the locality where the surface net was set.

Even before their emergence, mayflies form a portion of the ciscoes' food but they seem to be taken only in late nymphal instars, presumably due to some change in the insect's activity in those stages. Fish taken in early May in West bay ([11, 6], figure 1, opposite p. 10), where the water is only 15 feet deep, were found to be feeding on mayfly nymphs in fair numbers. Fish taken in deeper water (45 feet) at the same time, had only small quantities of plankton crustacea in their stomachs. At this date the concentration of fish was the greater in 15 foot water. It seems very probable that the availability of this important article of diet governs, to a large extent, the distribution of the cisco population in the spring. Mayflies may become available later in the deeper water, and the fish, if feeding on them, would tend to move from shallower to deeper water in early summer.

It is perhaps only fortuitous that this early movement brings the ciscoes into the vicinity of the deep water in mid-July so that they may enter the hypolimnion when the epilimnial temperature rises too high. As a matter of fact, there is some evidence that a few fish may be trapped in a minor depression in the west arm of the lake (figure 1, opposite p. 10). In this region there are two depressions, one fairly extensive in area [3, 5], with a depth of about 30 feet, the other somewhat deeper (45 feet) in the restricted channel in which the lake terminates to the west [1, 6]. On July 16, 1930, a few fish were taken in the ten yard water at [3, 5]. On August 24, 1932, a large cisco in a dying condition was taken from a gull over the deeper water at [1, 6]. This fish must have gone into this deeper water and have been forced out by stagnation or by the scouring out of the cold water by a seiche. The following year on August 17, 1933, nets were set on bottom in this locality but no fish were caught.

Once the fish have passed into cooler water they seem to be restrained from leaving it by the sharp rising temperature gradient of the thermocline. In late summer the fish retreat before a descending thermocline, although the temperature of the epilimnion has dropped below the upper limit of tolerance which the fish displayed earlier in the summer.

In spite of the fact that the thermocline appears to be such a barrier, the fish do pierce it eventually and leave the hypolimnion some time before the fall turnover. During early September in 1934 and 1935, fish left the bottom water and were concentrated just below the thermocline. This is seen particularly clearly in the "oblique" series of September 4 to 9, 1935 (figure 7, p. 26). This upward movement is correlated with a decrease in the oxygen coupled with an increase in carbon dioxide near the bottom in the hypolimnion.

The precise time at which the fish migrate from the hypolimnion would seem to be governed by a balance of forces acting on the ciscoes. Below, unfavourable concentrations of dissolved gases urge them upward. Above, a steep temperature gradient blocks their way. Their salvation lies in being able to stay within the frying-pan until the fire has died away to embers.

HORIZONTAL DISTRIBUTION

An idea of the horizontal distribution of the ciscoes in lake Nipissing may be inferred from a knowledge of their vertical distribution, and of the relief of the lake's basin. This inference must be drawn with reservations, for various reasons. In the first place, the fish present in a given stratum of water are not randomly distributed throughout the whole lateral extent of that stratum. On the contrary, their distribution is influenced by the relation of that stratum to the bottom. For instance, in the deep and shallow water series during the middle of June, 1935, 59 fish were taken between 30 and 45 feet in water 45 feet deep, while only 14 were taken in the same stratum at station 4, over water 150 feet deep. Conversely, later in the summer, fish were taken in the upper waters over station 4, while none was taken at the shallow water station.

For these reasons no precise indication of the lateral distribution of the fish has been attempted. Figure 10 shows, in a general way, the probable areas populated by the ciscoes at different times of the year. In May and early June the fish wander over most of the lake. By July they have become

concentrated in something like a third of the area, and are mainly in the eastern section. There are two localities in the western end where the water is of moderate depth ([3, 5] and [1, 6], figure 1, opposite p. 10), where ciscoes are known to occur in July. There is also a small basin over 30 feet deep in Cal-

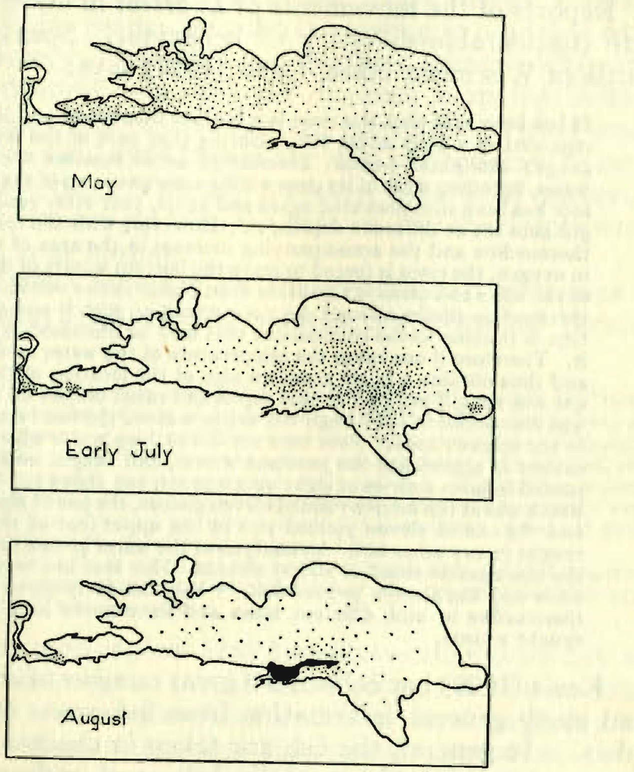


FIGURE 10.—Seasonal changes in the horizontal distribution of ciscoes in lake Nipissing.

lender bay [25, 5], at the eastern end of the lake, which has not been sampled.

In August practically all the fish have descended below 60 feet. This movement results in a tremendous concentration in the region shown in black in the lower panel. The whereabouts of the fish which withdrew in July into the more moderate depressions is problematical; it is possible that in some years at least they are destroyed by the warming of the water.

SUMMER DISTRIBUTION IN OTHER LAKES

Reports of the movements of *L. artedi* in other lakes indicate considerable diversity of behaviour. Speaking of the southern Wisconsin lakes, Cahn (1927) says:

> It has been said that the cisco is a bottom inhabitant and that it must be regarded as a deep water fish. During that part of the season when the oxygen conditions permit, *Leucichthys artedi* remains normally in deep water, spending most of its time within a metre or two of the bottom. This fact has been demonstrated again and again, year after year, by the use of gill nets set at different depths. . . . However, with the formation of the thermocline and the accompanying increase in the area of water deficient in oxygen, the cisco is forced to leave the bottom waters of the deeper parts of the lakes and assume a position even higher in the vertical scale. As the thermocline climbs upward the cisco comes up with it and assumes a position in relation to the thermocline that may be described as directly above it. Therefore if one takes the temperature of the water at different depths and thus obtains a fairly accurate idea of the location of the thermocline, one can set gill net just at this depth and catch ciscoes all summer. This was discovered in 1916 when the writer wanted the fish for an examination of the summer food. Nets were set in the deep water where the fish were caught in abundance the previous winter, and caught nothing. After repeated failures a series of eight nets was set, one above the other. The net which was at ten metres yielded eleven ciscoes, the one at nine yielded none, and the one at eleven yielded two in the upper foot of mesh; none were caught in any other net. An analysis of the water at this time showed that the thermocline stood at eleven metres. This idea has been followed ever since and has always yielded fish. I have set forty-three nets below the thermocline in nine different lakes and have never in a single instance caught a cisco.

Koelz (1929) has collected a great number of catch records and much general information from fishermen on the great lakes. In general, the fish are taken in shallow water until June and to a certain extent in July, and in deeper water in August.[5] They return to the shallower parts again in autumn.

[5]In all state of Michigan fisheries in great lakes waters, November is the month of maximum production of herring. In some waters (lake Superior, Saginaw bay) as much as 70-75 per cent. of annual catch is taken in the fall fishery (October through December). A secondary peak of production occurs in May and June. In most fisheries, the summer production of herring is relatively unimportant. The extreme condition is found in Saginaw bay, where in the two years, 1934-1935, the three months, July, August, and September, accounted for only one-half of one per cent. of the total catch of herring (Hile, personal communication).

There is some evidence that in lake Superior the fish never leave the shallow water. Koelz correlates this with extremely low surface temperature of that lake (Max. found by him 16.3°C.). In some years good catches of ciscoes have been taken by pound net fishermen in lake Erie throughout the summer. This Koelz also attributes to cool surface waters in those particular years. It is also interesting to note that when the cisco fishery of lake Erie had declined, better catches were made by floating nets up some distance from the bottom. This concentration of ciscoes at an intermediate level would indicate a vertical distribution like that in Nipissing (figure 7, p. 26), where there is usually a greater number of fish swimming some distance up from the bottom over the deeper water than there is at bottom.

Scott (1931) reported on the distribution of ciscoes in some Indiana lakes and he records the following peculiar behaviour:

> Early in September, usually between the first and the tenth, the "cisco" . . . come to the surface of Snow Lake, struggle as if in discomfort, and then disappear. They have been described by local observers as "gasping for breath". When they begin to appear a maximum is soon reached, after which the number at the surface is rapidly reduced. The maximum rarely lasts more than a day and the whole phenomenon is over in less than a week. This has been observed on Snow Lake for at least thirty years. It occurs occasionally on the third basin of James Lake.
>
> They have been examined repeatedly for parasites without success.
>
> I suspected that the disappearance of the oxygen from the hypolimnion might be the cause.

He goes on to explain that he believes that these fish are trapped by an oxygen "notch" developing at the thermocline until they become asphyxiated and float up through it after they have lost control of their hydrostatic apparatus.

Scott, in collaboration with Hile, found ciscoes living under very unusual temperature conditions in the epilimnion of Indian Village lake and the latter suggests (Hile, 1931) that these fish may constitute a distinct race.

Hile (1936) discusses the vertical distribution of the cisco in Trout, Muskellunge, Silver, and Clear lakes, all in the north-eastern highlands, Wisconsin. He gave particular attention to the question of the relationship between the vertical distribution of the cisco and the temperature and the oxygen concentration in the different lakes. Several extracts from Hile's report (pp. 258 *et. seq.*) follow:

> . . . in Trout Lake in middle and late summer there lies below the depth of 10 or 12 meters a large body of cold water with a good supply of oxygen. It is in this region that the cisco lives during this season of the year, . . .
>
> It is in Muskellunge Lake that the late-summer habitat shows the most marked restriction to a limited stratum . . . (ciscoes) were not plentiful in depths less than 9 meters and were absent in the deeper portion of the hypolimnion. [Aug. 27-29, 1930] . . .
>
> The results of the rather extensive fishing of the 1932 collecting season . . . give the most complete information concerning the vertical distribution of the cisco in Muskellunge Lake . . . as a result of . . . deficiency of oxygen in the deeper strata the ciscoes are forced out of the cooler strata and by reason of their preference for cool water and their need of oxygen become concentrated in that stratum of water that has the lowest temperature available and yet contains sufficient oxygen to support life. . . .
>
> The Silver Lake cisco agrees with the Muskellunge Lake cisco in showing a rather sharply delimited vertical distribution. . . . Thus in late summer the Silver Lake cisco is confined to a narrow stratum in the upper part of the hypolimnion and the lower part of the thermocline. . . .
>
> The field records of lifts of ciscoes in Clear Lake indicate that in this lake the cisco occurs in all parts of the hypolimnion from midsummer to early autumn. . . at this time of the year there is in Clear Lake a plentiful supply of oxygen at all depths.

Apparently conditions in lake Nipissing are somewhat intermediate between those existing in lakes where there is a rapid depletion of oxygen in the hypolimnion and those existing in the great lakes. In the former lakes the whole summer migration is probably slurred over by the rapid stagnation of the hypolimnion. In the great lakes, on the other hand, the temperature of the upper strata may never rise above the limits of tolerance exhibited by this species, and the migration may never take place.

THE RELATION OF AGE TO VERTICAL DISTRIBUTION

In the 1934 series at station 3 (figure 5, p. 22) it was found that the average size of the fish taken in shallow water during May, June, and July diminished progressively in spite of the fact that this was the growing season. Figure 11 shows that this was due to changes in the age composition of the fish in this vicinity. In the earliest catch (May 15-17) the age fre-

quency distribution was bimodal with IV-group and VII-group fish predominating. In the next catch, a month later, the older fish had largely disappeared and the curve was unimodal with the mode at group IV. The remaining panels indicate a further lowering of the average age to a minimum

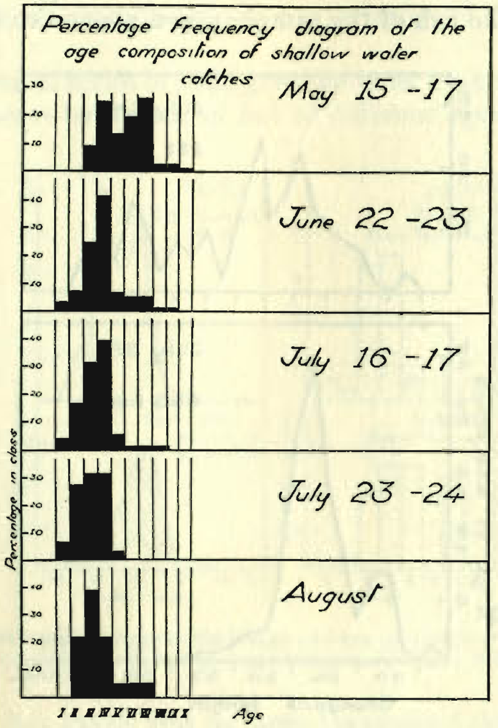


FIGURE 11.—Changes in age composition in catches taken at station 3, 1935. The total number of individuals in the samples analysed in this figure are given in table 6, p. 23.

in August. It will be noted that a few old fish reappeared in the August samples. Catches taken in deep water on July 14 and July 28, 1932, also showed that the larger (older) ciscoes entered the deep water earlier than did the smaller (younger) fish (figure 12).

When the ciscoes are leaving the hypolimnion it is the younger fish which leave first. Catches above and below the thermocline at the end of the summer in 1933 and 1934 illustrate this fact (figure 13).

The 1934 catches were taken when the upward migration was under way and the probability is very great that the fish taken above the thermocline had but recently left the hypolimnion. The fish of the sample taken above the thermocline

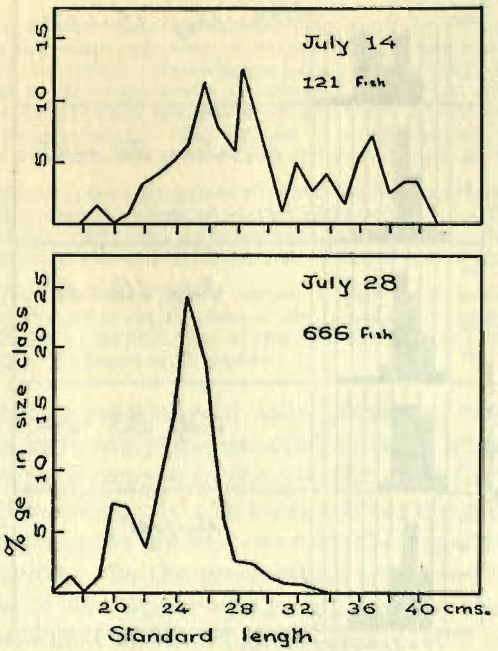


FIGURE 12.—Changes in length composition in catches of ciscoes taken on the bottom at station 4, 1932.

had a much lower average age than those of the one taken below. The 1933 figures show another aspect of the same phenomenon. The results in this year show the earlier disappearance of the smaller (younger) fish from the deep station and its immediate vicinity. The upper polygon gives the length frequency composition of a catch taken at station 4 in the middle of the summer. This curve is bimodal with peaks

at 22 and 26 cm. The lower panel shows the size composition of two catches, one at station 4 and the other at station 6 (figure 6, p. 24). These samples were taken later in the season than those of 1934 and represent the last of the upward migration. For that reason there is no difference in their size composition. These samples show a unimodal distribution representing largely the upper range of the fish taken on July 25.

The vertical series of 1935 give the most connected picture of the different behaviour of fish of different ages. Since the

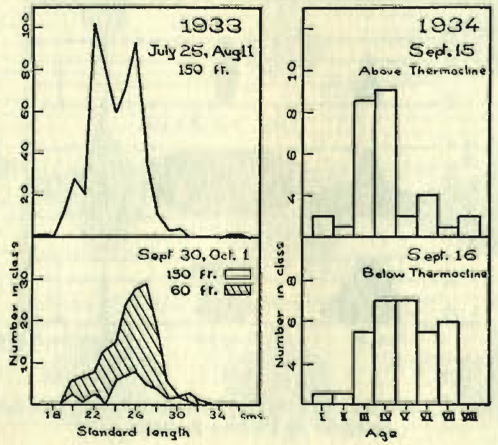


FIGURE 13.—Seasonal changes in the length and age composition in ciscoes taken on the bottom, station 4 and vicinity, 1933 and 1934.

number of fish taken was so large (between 5,000 and 6,000 specimens) they will be discussed according to size instead of age groups. The results of the major portion of this fishing are given in tables 7 and 8.

Figure 14 illustrates the vertical distribution with respect to size of the fish taken in the shallow water series at station 3 (p. 22). The fish have been grouped into three arbitrary size classes: smaller than 20 cm., from 20-25 cm., and longer than 25 cm. These groups will subsequently be referred to as "small", "medium", and "large" fish.

In the June 13 series there were more large fish taken than either medium or small. On July 10, the number of fish taken increased, but this increase was due largely to the presence of large numbers of medium fish. In this series it will be noted that fish longer than 20 cm. have the mode of their distribution in the upper 15 feet, whereas the fish smaller than 20 cm. are concentrated more in the 15-30 foot stratum. This difference in position is correlated with the feeding habits of the ciscoes at this date, the larger fish feeding on emergent mayflies, the smaller on plankton.

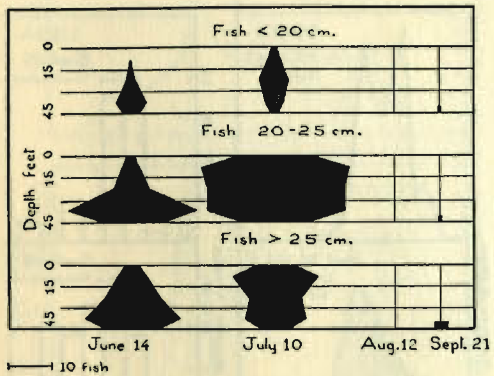


FIGURE 14.—Seasonal changes in vertical distribution in ciscoes of different lengths at station 3, 1935.

No ciscoes of any size were taken in the August series, due probably to the exceptionally high temperature of the epilimnion in this season (figure 8, p. 29).

The data for the ciscoes taken in the deep water series of nets are illustrated in figure 15, which is based on data given in table 8, appendix 1. Medium and large fish caught in the smallest mesh have been omitted. An estimated distribution is shown for July 17, based on the results of an incomplete series of net settings.

The few fish taken over the deep water in June were mostly longer than 26 cm. These large fish were not concentrated below the thermocline, which at that date was between surface and 15 feet, but they were in water cooler than 15°C. The catch taken from July 3 to 6 shows about the same distribution of sizes except that the large fish had dispersed downward to the bottom.

By July 17 there was a tremendous increase in the number of the fish taken in the region of the thermocline. Practically all these fish were longer than 20 cm. and more than half of

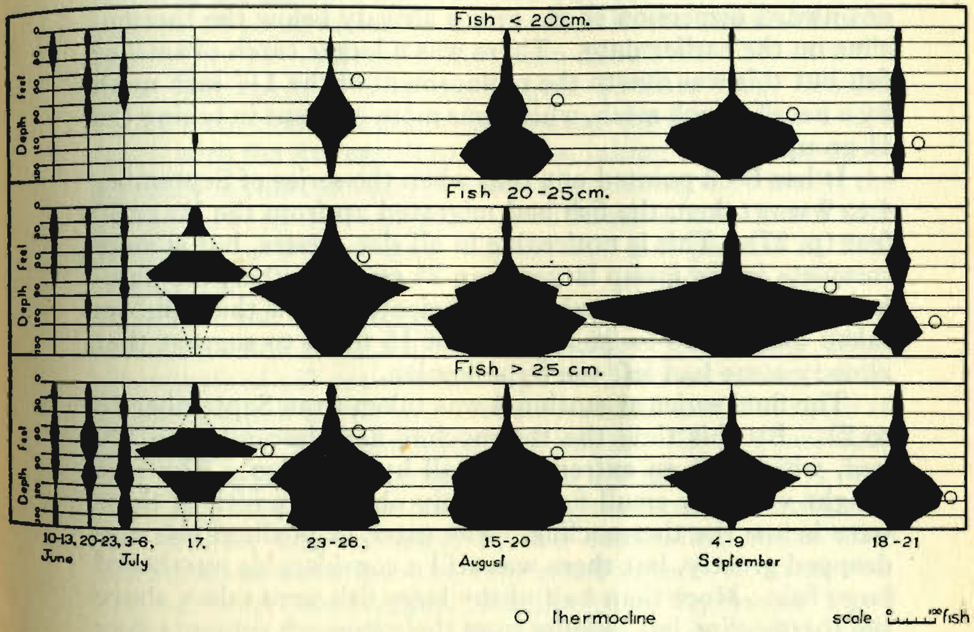


FIGURE 15.—Seasonal changes in vertical distribution in ciscoes of different lengths at station 4, 1935.

them were over 25 cm. in length. No small fish were taken in the fine mesh in the bottom 30 feet. In the series of July 23 to 26 there was a further increase in number of large fish taken but it would seem likely that this increase was the consequence of those large fish already below the thermocline on July 17 becoming more concentrated in the lower strata, rather than to a further influx of ciscoes of this size range. On the other hand, the medium fish showed a marked increase in numbers in the region just below where the thermocline had been on July 19, which must have been due to a further immigration. It will also be seen that considerable numbers of small fish had migrated to the deeper water.

It is probable that most of the population had migrated to the hypolimnion by July 26. The distribution of the fish taken in the August 15 to 20 series seems to indicate a gradual downward dispersion of the group already below the thermocline on the earlier date. There was a larger catch of smaller fish but this was due to the replacement of the 1½ inch mesh by a net of 2 inch mesh, which was more efficient in taking the II-group.

It has been pointed out that when the series of September 4 to 9 was taken, the fish had migrated up from the lower 30 feet (p. 27). This is noticeable in all size classes, but is more complete in the group larger than 25 cm. Further, the number of large fish captured was sufficiently below the numbers taken on July 23 to 26 and August 15 to 20 to suggest that already some had left the hypolimnion.

The final series at station 4 was taken from September 18 to 21. By this time the thermocline had descended to 120 feet, which left an extremely small hypolimnion. The nets caught very few small fish and only about one-fifth of these were below the thermocline. The catch of medium fish also dropped greatly, but there was still a considerable number of large fish. More than half of the large fish were taken above the thermocline but judging from their stomach contents they had only recently left the hypolimnion (Langford, 1938).

In figure 15, in which the fish are massed into three large divisions, there is an apparent anomaly in the behaviour of the large fish. This figure shows that although the proportion of large fish decreased in the September 4 to 9 series, it rose again in the series of September 18 to 21. If these changes in numbers were due to migration, this must mean that a certain section of the group called large fish migrated early, while another remained in the hypolimnion until last of all. Figure 16 supports this view. This graph is constructed from table 9, which gives the length frequency distribution of the medium and large fish taken in the last four series at station 4. The object of the graph is to compare the changes in size composition taking place in these catches. The number of each length class taken in the July 23 to 26 series has been taken as unity, the whole catch being thus represented by a rectangle of unit height erected over the July 24 date line. The ratios of the number of fish in each size class taken during the August 15 to 20 series, to the number in the same size class of the July 23 to 26 catch, have been calculated. These ratios have been plotted over the August 16 date line. Similar ratios have been calculated comparing the September 4 to 9 catch with the August 15 to 20 series, taking the August series as unity in this case, and plotted at September 6. Finally, the ratios between the September 18 to 21 series and that of September 4 to 9 have been worked out and plotted at September 19.

Where the ratio in figure 16 rises above unity an increase in catch is indicated; where it drops below, a decrease. Since the results of gill net settings represent concentration, an increase in catch is due to a further restriction of the range of the section of the population in question. In this case such an increase is due to a concentration brought about by, first, fish rising from the bottom and being concentrated under the thermocline, and secondly, by the descending thermocline forcing them down into the very small volume of water over 120 feet deep (note vertical distribution on September 4 to 9 and 18 to 21, figure 15, p. 41). A decrease in catch, on the other hand, is indicative of an increase in range, and may be considered to show a migration from the restricted hypolimnion to the extensive epilimnion.

In the graph it will be seen that as early as the middle of August there is a decrease in the catch of ciscoes from 25.0 to 28.9 cm. long, and that the largest fish have become more concentrated. This concentration is just below the thermocline. By the beginning of September more fish had disappeared over the size range from which fish had disappeared in the August catch, and in addition to these, some of the largest fish had gone, and there had also been a loss in the 24.5 cm. group. It will be noted further that at this time the smaller size classes were beginning to concentrate below the thermocline. By September 18, practically all fish below 25 cm. had migrated and most of those from 25 to 27 cm., leaving only the largest remaining in any numbers.

Apparently the fish migrate out in the order in which they come in, except for those that come in first of all. In this

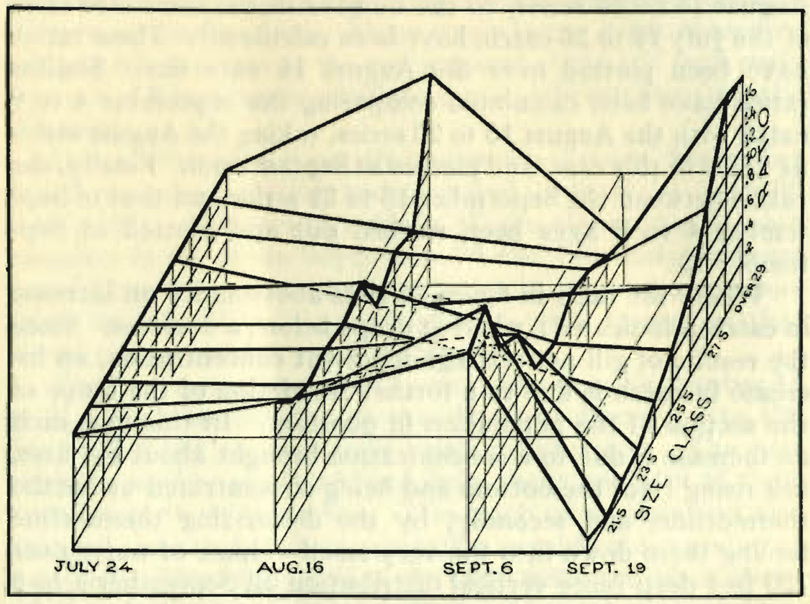


FIGURE 16.—Changes in length composition in vertical samples of ciscoes taken at station 4, 1935. For explanation see text, p. 43.

group the very largest ciscoes predominate. It is quite natural that these particular fish should remain in the hypolimnion, since even as late as September 18, the temperature of the epilimnion was probably higher than when the fish had left it in the spring.

This order of migration with respect to age can be considered to be the result of a decreasing tolerance with increase in age towards the factors effecting migration. Older fish are

more sensitive to high temperatures and to unfavourable concentrations of dissolved gases. The balance between these factors decides the time of the return to the epilimnion; the largest fish remain longest in an uncomfortable hypolimnion since movement upward brings them into a temperature undesirably high.

A change with respect to age in the ability of certain fish to withstand high temperatures has been shown (Huntsman and Sparks, 1924), and it is possible that ciscoes may also behave in this manner. A similarity drift in sensitivity towards low oxygen and high carbon dioxide is not so clear (Wells, 1913; Gutsell, 1929). Wells found, when fish of different ages were exposed to conditions where the concentration of oxygen was low and that of carbon dioxide was high, that small fish succumbed earlier than large fish. Gutsell's experiments in which the concentration of oxygen was not so low gave conflicting results. There is a possibility that the reaction of the fish towards low concentrations of oxygen may differ from their reaction towards high carbon dioxide.

A difference in sensitivity to carbon dioxide correlated with age, and possibly sex, was found in a single experiment performed with Mexican sword tails *Xiphophorus helleri*. The results of this experiment are given in table 10. Three fish

TABLE 10.—Age differences in the rate of asphyxiation of Mexican sword tails subjected to carbon dioxide.

Order of asphyxiation	Size	Sex
1	large	male
2	large	male
3	small	?
4	large	female
5	small	?
6	small	?

about one month old were placed together with three other fish just approaching maturity and carbon dioxide bubbled through the water in which they were placed. Five of these fish became asphyxiated in the order given in the table—the sixth, a small one, was still conscious when the experiment was discontinued. The results of this experiment differ from those of Shelford and Allee (1913), who make the general statement that the young were more easily affected by the various stimuli employed than were the adults of the same species. Among these stimuli were high concentrations of carbon dioxide. In the specific instance they describe (p. 258) they attribute this difference in part to the large fish having too great a momentum to exhibit the reaction.

DISTRIBUTION OF YEARLINGS AND FINGERLINGS

The accompanying graph (figure 17) illustrates our knowledge of the August distribution of the O-group and I-group.

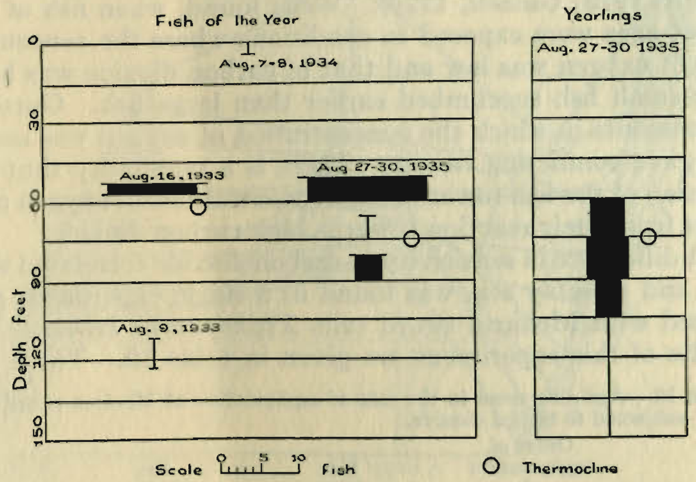


FIGURE 17.—Vertical distribution of zero- and one-group ciscoes in August.

Ciscoes of the O-group were fished for in August in 1933, 1934, and 1935, and were found in the region of the thermocline.

The vertical distribution of the I-group fish has been given for 1935, the year in which the oblique catches were made. A special series in which 50 yard units of 1½ inch mesh were used, was set for these yearlings between August 27 and August 30. Fishing was confined to strata below sixty feet. These fish were also in the vicinity of the thermocline, but somewhat lower than the fingerlings. None was taken in water below 105 feet. Figure 17 may be compared with

figure 15 where the distribution of fish below 20 cm. is shown; the majority of these fish belong to group II.

The fingerlings are perhaps more consistent in remaining above or near the thermocline. In some seasons, 1934 for instance, numbers of year old fish have been taken on or near bottom in the hypolimnion.

THE RELATION OF SEX TO VERTICAL DISTRIBUTION

Bottom Samples

A consideration of the sex ratios in various catches makes it seem probable that males respond more positively than do females to the agents bringing about the summer migration. For instance, in 1931 two catches, taken by the same graded series of nets, were lifted from the deep water at station 4 on July 14 and August 13 respectively. In the earlier catch the ratio of males to females was 65 to 25, while in the setting of August 13, 75 males and 83 females were taken. It would seem apparent that the migration up to July 14 had consisted largely of males, while there had been an influx of females after this date. Bearing in mind the fact that fishes of different sizes migrate at different times, it will be evident that there is a possibility that the change in sex ratio may have been due to a change in size composition. This, however, is not true. The length composition curves of the two sexes in each catch, given in the accompanying figure (figure 18) show that the increase in the number of females occurred generally over the whole size range.

A parenthetical remark might be inserted here to the effect that these two catches do not strictly record the progress of events in one definite stratum. It happened, since the net was set up the steep side of the "deep hole", that the nets with larger mesh were in water as shallow as sixty feet on July 14. This accounts for the absence of large fish in the catch on this date.

Apparently the age of the individual determines its response to a greater degree than does its sex, for the change in sex ratio is not so simple a trend as the change in size composition. In the two catches at station 4, taken on July 14 and July 28, 1932, there was, if anything, a decrease in the proportion of females. On July 14, 55 males and 63 females were taken; on July 28, 335 males and 331 females. At the same time there was a great change in the size composition of the catches. In the earlier sample large fish predominated, while in the later there were great numbers of smaller fish (figure 12, p. 38). Thus, while it may be probable that large males were the first to migrate to deep water, it is evident that the large females must have followed them some time before the smaller fish descended.

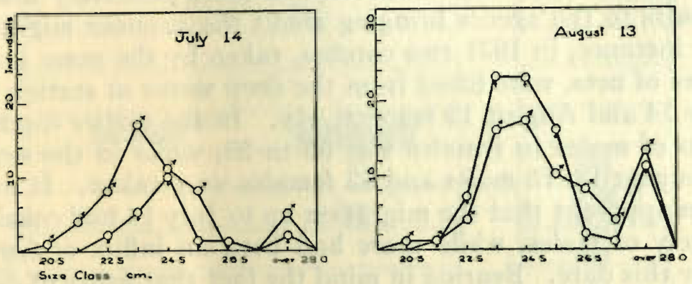


FIGURE 18.—Changes in length and sex composition in catches of ciscoes taken at station 4, 1931.

Just as the very large fish which were the first to enter the hypolimnion were the last to leave it, so does the proportion of male fish increase again in the late samples taken below and in the vicinity of the thermocline. In 1933 the midsummer sample taken on July 30 at station 4 contained 238 males and 279 females. Catches made in this vicinity on October 1 and 2 consisted of 77 males and 79 females. These differences are statistically significant, the difference between the percentages being 2.6±.05.

Similar conditions were found in the 1934 samples. In the catches above and below the thermocline taken on September 15 and 16 the ratio was 36 males to 33 females, while females predominated in the August catch.

Vertical Samples at Station 4

The composition of the samples taken in the oblique series illustrates the behaviour of the sexes exhibited in the isolated cases discussed above, in a manner that allows of a connected treatment of the changes from spring to fall. Tables 8 and 9 give the numbers of each sex taken in the different series, first with respect to depth, and secondly with respect to size. The trend in the percentage of males and females in all the fish longer than 20 cm. taken at station 4, is illustrated in figure 19.

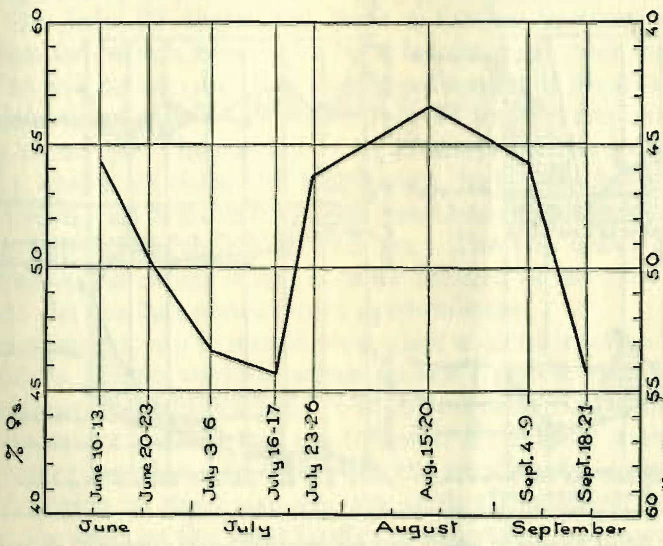


FIGURE 19.—Changes in the relative numbers of males and females in ciscoes longer than 20 cm. taken in oblique series at station 4, 1935.

In the first sample taken June 10 to 13 there were more females than males. The percentage of males increased steadily until July 17. After this date there was a sudden increase in the proportion of females which was followed by a further gradual increase, the peak being found in the series of August 15 to 20. Following this there was a slight falling off in the proportion of females by September 4 to 9, and after this date there was a very sharp decrease between that series and the final one taken over the period September 18 to 21.

In an attempt to clarify this rather complex change in sex ratio, figure 20 has been prepared. This diagram is an attempt to illustrate the changes in the numbers of each sex in different size classes. It is merely an extension of the principle employed in constructing figure 16 (see p. 43 for details). The left panel shows the influx of fish to station 4 in June and July. The number of each sex in each length class in the June 10 to 13 series has been taken as unity. In the upper diagram

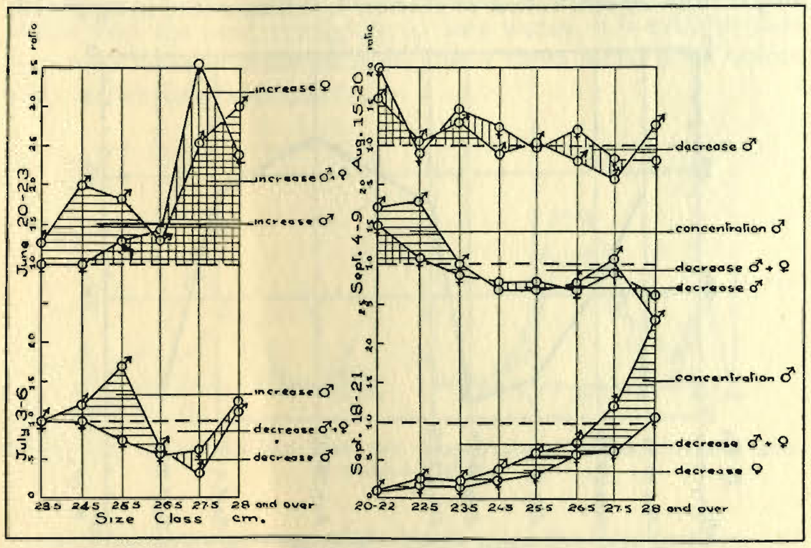


FIGURE 20.—Changes in length and sex composition in catches of ciscoes taken in oblique series at station 4, 1935. For explanation see text, p. 50.

the catch of June 20 to 23 has been compared with the earlier series. It will be seen that while roughly twice as many males between 23 and 26 cm. were taken as on the previous date, there was practically no increase in the number of females in this size range. On the other hand, in the larger sizes there was a greater increase of females than of males. Between June 23 and July 3 there was a general decrease in the number of female fish of all sizes except the largest. The number of males had increased in the central length classes. The de-

creases noted are probably due to the cooling of the epilimnion that happened to occur between these dates, causing the fish above the thermocline to scatter. The increase in males would indicate that still more fish of this sex had moved below the thermocline.

The incomplete series of July 17 could not be included in this graph but it will be remembered from figure 15, and previous discussion (p. 41), that on this date there was an enormous increase in numbers of large and medium fish. Among these fish there was a high percentage of males (table 8). By July 23 there had been a further increase in the medium fish which must have been for the most part females.

The migration out from the hypolimnion is illustrated in the right-hand panel. Here the July 23 to 26 series has been taken as unity. The August 15 to 20 sample shows a decrease in the males in some of the upper, but not the largest, size classes. By September 4 to 9 there had been a general loss in the size classes as low as 23.5 cm. The two lower graphs show a concentration which is more decided in the case of the males. In the last series males predominate.

In summing up it would seem that a consideration of the sex ratios of the various series makes possible this further description of the migration. The largest male ciscoes migrate to deep water earliest and are followed by smaller males and the largest females. In their turn the smaller ciscoes migrate in, according to their size and sex with the smallest females being the last, or the least likely, to migrate. In leaving the hypolimnion the last to leave are those male fish which entered earliest.

Changes in Sex Ratios in Catches at Station 3

This is the station in water of medium depth (45 feet) where the ciscoes accumulate before descending below the thermocline. The changes in numbers at this station have been discussed on pages 23 *et seq.* Table 11 gives the number of each sex taken in 1934 and 1935.

The catches in the middle of July show a predominance of males in both years. This would seem to indicate that the fish are partly limited in their movements by temperature conditions before they descend below the thermocline. That is, while all fish taken in the epilimnion may still be feeding, even at the surface, some may be more restricted in their movements than others, due to their inability to stay as long in the upper warmer water. Females which are apparently less sensitive than males, may still be moving over wider areas. Males while able to feed even in the surface waters, may be more restricted in that they must descend occasionally to cooler water.

TABLE 11.—Sex ratios at station 3.

1934 Date	May 15-17 ♂	♀	June 23 ♂	♀	July 17 ♂	♀	July 24 ♂	♀	August ♂	♀
Small	..	..	6	9	18	13	4	4	..	2
Medium	16	10	36	33	53	46	6	13	4	1
Large	22	15	8	8	8	10	..	1	1	2
Total	38	25	50	50	79	69	10	18	5	5

1935 Date	May 15-17 ♂	♀	June 2 ♂	♀	June 13 ♂	♀	July 10-11 ♂	♀
Small	..	3	25	14	3	3	8	5
Medium	29	50	48	45	21	21	73	55
Large	13	18	9	9	21	22	27	41
Total	42	71	82	68	45	46	108	101

The earlier movement of the older fish towards deep water is perhaps indicated by the fact that females predominate in the large fish taken in July in shallow water, while males are in the majority among the medium fish. The actual percentage of females is 59 per cent. of the large fish and 44 per cent. of the medium; the difference between these two percentages is 15 ± 6 per cent., which is statistically significant.

The July 24, 1934, sample, taken after most of the fish had left shallow water, shows a preponderance of females, but the sample is too small for the sex ratio of 10 males to 18 females to be accepted as trustworthy.

Early Catches in Shallow Water

In 1935 four samples were taken by gill nets in water 15 feet deep in West bay ([11, 6], figure 1, opposite p. 10), over the period from May 15 to May 31. In these, 129 females and 120 males were taken.

ANNUAL DIFFERENCES IN MIGRATORY ACTIVITY

As may be expected, there are differences in the dates when the population moves in different years. Evidence for these annual fluctuations has appeared at various times during the previous discussion. In this section it is brought together in an orderly manner. The accompanying table (table 12) summarizes the differences found in the several years.

TABLE 12.—Annual differences in the migration of the ciscoes to the hypolimnion.

Average July temperature 0-30 feet	Rank	Year	Migratory activity
21.1°C.	1	1934	Fish left shallow water between July 16 and 24.
21.1	1	1931	Fish left shallow water by July 9.
20.8	2	1933	Fish left surface suddenly July 10.
20.5	3	1935	Large migration to deep water between July 17 and 24.
19.4	4	1930	Fish still in shallow water on July 25.
19.0	5	1932	Fair numbers still at surface at the end of July.
18.3	6	1929	Many ciscoes still in 45-60 foot water on July 30. Least oxygen depletion in hypolimnion. Records inadequate but migration probably very incomplete.

Since it seems probable that temperature is the major agent in bringing about this migration, the years have been arranged in order of the average temperature of the upper 30 feet of water for the month of July. There are only sufficient data for the discussion of the downward movement.

In four of the seven years the ciscoes had vacated the shallow water by about the middle of July. In the other three they were still present, at least in fair numbers, by the end of that month. These differences in the time of migration are correlated closely with the average temperature in the shallow water. The correlation, however, is not absolute; it would seem that if the temperature reaches a certain maximum, migration takes place. Below that temperature migration is incomplete or delayed.

FEEDING ACTIVITY

Introduction

In 1935 the alimentary tracts of all fish captured in the oblique series were examined and the contents of the stomachs analysed. This somewhat extensive task was accomplished through the co-operation of Dr. R. R. Langford, who was engaged in an investigation of the plankton of the lake. Dr. Langford is reporting the results of the stomach analysis, and his paper (Langford, 1938) will be referred to here as occasion requires. In working over the material, it was noticed that the fish sometimes had their alimentary tracts completely empty, even of parasites. (The pyloric caecae were not examined.) It seemed evident that these fish had not been feeding for some time before capture. Fish "empty throughout" were recorded as such, and it appeared that whenever there were many fish without food in the stomach, the majority of these had the intestine also empty, except in the early spring when the fish were not feeding very heavily.[6]

Feeding in Shallow Water

In the early spring little food was found in the individual stomachs and there was a fairly high percentage of empty stomachs. As the season advanced more food was found per stomach and the number of empty stomachs dropped. In July practically all the fish taken in shallow water contained food. At this time, when taken at night, they were found gorged to repletion with winged mayflies. The few individuals whose stomachs were empty had apparently ceased feeding. With the appearance of these non-feeding fish in the catches, the number of fish taken in shallow water dropped.

[6]For fuller discussion of the relation of the volume of stomach contents to feeding see Langford (1938).

Feeding in Deep Water

There is a close connection between the migration to the hypolimnion and the presence of fish which are "empty throughout" in the catches. Whenever an increase was found in the numbers of fish taken in the hypolimnion during the downward migration, that increase was correlated with an increase in the number of fish captured in which the alimentary tracts were completely empty of food. In the previous section it was pointed out that in July a few such non-feeding fish were found in the shallow water catches at station 3, and it was suggested that the fish stopped feeding just before migrating. Confirmation of this belief was found in the July 17 series of station 4, in which a sudden increase occurred in numbers of fish taken below 45 feet. In this series there were large numbers of non-feeding fish in the nets just above the thermocline. This sample was apparently taken from the population just as it was descending to the hypolimnion.

In order to illustrate this relation between feeding activity and the downward migration and to show further features occurring later in the summer, figure 21 has been prepared. In this graph the vertical distribution of the fish taken at station 4 is shown. Samples taken in each 15 foot stratum have been grouped into two classes: fish whose stomachs contained at least a trace of food—fish with "full stomachs", and fish whose stomachs were empty—fish with "empty stomachs". The latter fish were in the main "empty throughout", and there is little error in considering this group as a whole to be non-feeding fish. In the graph, fish with "full stomachs" are indicated in black, and those with "empty stomachs" by a white rectangle.

Since there are differences in the rate of migration of fish of different sizes, the ciscoes taken have been grouped into the "small", "medium", and "large" groups used previously (p. 39). The feeding activity of these groups will be dealt with in the order in which the groups migrate to the hypolimnion.

It should be noted that in order to show up the small catches of June and early July the first three series are plotted on three times the scale used for the later samples. (See appendix 1.)

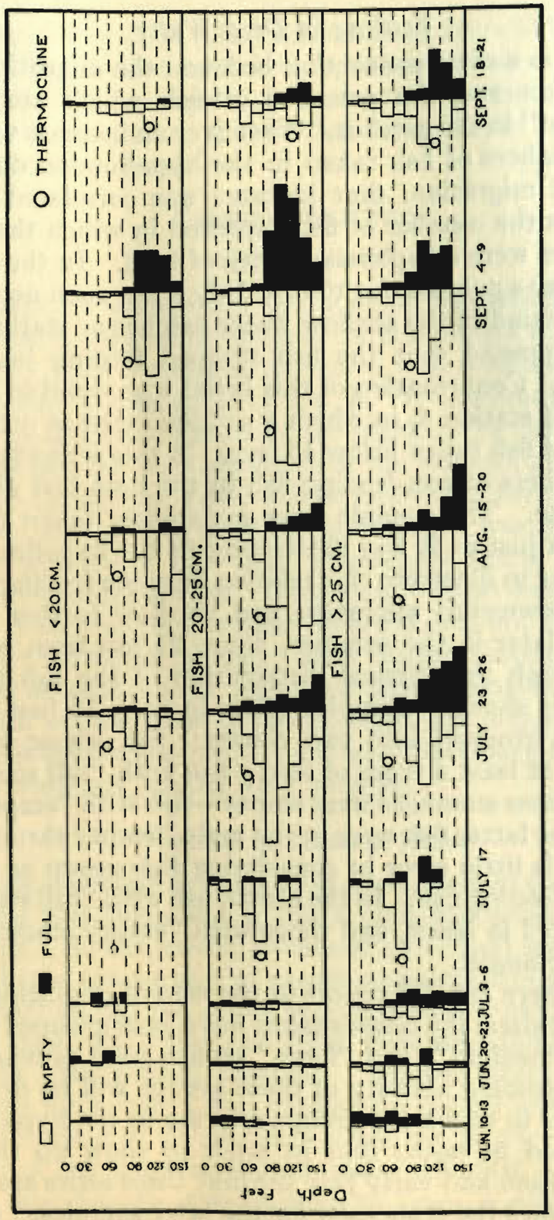


FIGURE 21.—Vertical distribution of ciscoes with and without stomach contents at station 4, 1935.

(a) **Large Fish.** The large fish are the earliest to arrive in any numbers in the vicinity of station 4. In the first series, taken June 10 to 13, most of the large fish were found in depths of less than 105 feet. At this date the thermocline was not as yet established. The fish were probably all feeding, for no fish "empty throughout" were noted and the few fish which had empty stomachs had in all likelihood digested, before the net was lifted, the food that had been in their stomachs when captured.

By June 20 when the next series of nets was set, there had been a considerable increase in the numbers of large fish in this locality. This increase equalled in numbers the non-feeding fish in the sample. Between June 23 and July 3 the surface waters cooled and there was apparently no further migration to deeper water. Ciscoes were taken in the July 3 to 6 series in about the same numbers as in the previous one. This time, however, most of the fish had stomach contents which would suggest that those fish which were not feeding about June 20 had begun to do so by July 3.

Coincident with the large increase in catch on July 17, there was a corresponding increase in the number of fish "empty throughout". It was in this catch that the majority of the non-feeding fish were just above the thermocline. In the July 23 to 26 series the majority of the fish were just below where the thermocline had been on July 19. In this catch a difference can be seen in the vertical distribution of feeding and non-feeding fish. Fish with stomach contents were found most abundantly close to the bottom; empty fish were taken in the greatest numbers in the upper hypolimnion.

In the August 15 to 20 series, feeding fish were still found in the greatest numbers at the bottom, but the non-feeding fish had scattered downward until they were fairly evenly distributed throughout the hypolimnion.

Two changes will be noticed in the early September series. A decrease in the proportion of non-feeding fish will be seen which means, presumably, that some individuals previously not feeding had started to feed. There had also been an upward shift in the population, which had resulted in the lowest 15 feet being vacated by all except a few non-feeding fish. It is difficult to decide whether there is a difference in the upward movement of the feeding and non-feeding groups, since the matter is complicated by the fact that already there had been a migration of some large fish from the hypolimnion (p. 43).

By the time that the last series was taken, September 18 to 21, many fish had left the hypolimnion. In this series feeding fish were found only in the vicinity of the thermocline, and those taken above the thermocline contained food which must have been gathered in the hypolimnion. Empty fish were taken at all depths. Among these there must have been both fish which had not been feeding in the hypolimnion and fish which, while they had been feeding in the hypolimnion, had on leaving it stopped feeding. The length of the period during which ciscoes do not feed after returning to the epilimnion in the fall has not been determined.

(b) **Medium Fish.** The feeding activity of the medium fish shows the same characteristics as were pointed out in the case of the large fish, but they differ in a degree corresponding to the difference in migration. Few medium sized fish were taken at station 4 during June and early July. The first time that they were taken in any numbers was on July 17, and in this series a large number of non-feeding fish were taken above the thermocline as in the case of the large fish. Between July 17 and 24 there was a further increase in the numbers of medium fish and there was again a corresponding increase in the number of non-feeding fish. The non-feeding and feeding groups in the medium class show the same vertical distribution as that found for the large fish on this date. In August the medium fish also behave in the same manner as the large fish.

In September there is again the upward shift of both feeding and non-feeding fish, and the increase in the feeding group. In the "medium" group very little migration to the epilimnion had taken place by September 4, and it can be seen that the feeding section of the population had shifted from the bottom to a greater degree than had the non-feeding group.

By the time that the September 18 to 21 series was taken, most of the medium fish had left the hypolimnion and they, like the large fish, do not feed immediately upon entering the epilimnion, since again the feeding fish were all found below or near the thermocline.

(c) **Small Fish.** In the data for the small fish there may be seen the same cessation of feeding before entering the hypolimnion, the same resumption of feeding in September, the same upward movement of feeding relative to non-feeding fish, and the same second lull in feeding activity on returning to the epilimnion, that have been described in the two larger size groups.

Comparison of the Feeding Activities in the Three Size Groups

It has been stated that the difference in feeding activity shown in the three groups is one of degree. The largest fish enter earliest and more individuals of this group feed in the hypolimnion. This can be seen when the proportions of feeding and non-feeding groups, taken in the July 23 to 26 series, are compared.

TABLE 13.—Comparison of feeding activity in the hypolimnion in different size groups of ciscoes taken, July 23-26, 1935.

Size group	Percentage of group with full stomachs
Small	19
Medium	38
Large	50

This correlation of feeding activity with time of migration can even be found within one group. It has already been pointed out that due to weather conditions at the end of June, migration did not proceed steadily, but practically stopped for a week or ten days after some of the largest fish had descended to the hypolimnion. This group of the large fish apparently resumed feeding within that length of time.

Large fish migrating later took much longer than this to begin feeding in the hypolimnion; those migrating after July 17 probably do not feed again until September.

Not only is the extent to which fish feed affected by the time of migration but the nature of the diet is also influenced. Fish migrating early feed almost entirely on copepods of two species and on *Mysis relicta* during the summer months. Due to the peculiar behaviour of *Diaptomus oregonensis*, a species in which the adults breed in the extensive epilimnion of lake Nipissing while the young, after considerable growth, descend in numbers to the hypolimnion, those fish which feed in the hypolimnion are able to obtain a plentiful supply of food. Late migrants, on the other hand, spend July in the epilimnion and feed well on the emerging mayflies at night and to some extent on daphnia during the day (Langford, 1938) but fast throughout August, and perhaps throughout September too.

The differences in vertical distribution of feeding and non-feeding fish observed in the small and medium classes in the September 4 to 9 series lend additional support to the hypothesis that the ciscoes which are most sensitive to high temperatures are also most sensitive to unfavourable concentrations of dissolved gases (p. 45).

THE RELATION OF THE SUMMER MIGRATION TO GROWTH

Introduction

The population is by no means homogeneous with respect to its migratory habits and feeding activities. This heterogeneity is due to the different response exhibited by fish of different age and sex or of different constitution. We have already seen that all individuals in the population do not share alike in the food present in the lake or even in one locality.

The temperature experiences of the various groups also differ to a marked degree. Those fish which migrate below the thermocline experience during the time the lake is free of

ice, two periods in which they are in warm water separated by an interval during which they are in quite cold water. The relative proportions of these warm and cold water experiences vary with the date at which the fish migrate. The accompanying graph (figure 22) illustrates the probable temperature experiences of certain groups during 1935. It is of necessity rather complicated by the crossing of lines because the temperature experiences of the groups are rather involved. The number of dots which break each line indicate the order in which certain groups entered the hypolimnion.

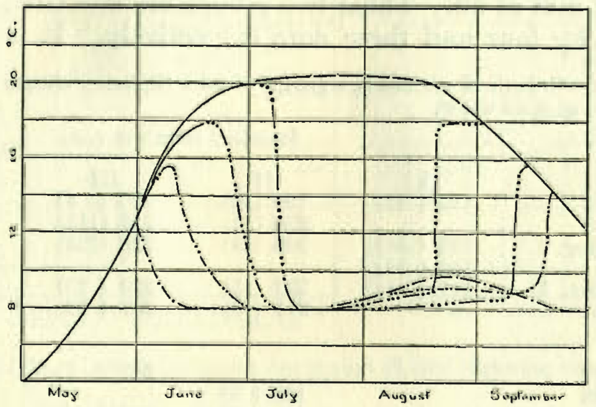


FIGURE 22.—Probable temperature experience of certain groups of ciscoes in 1935.

The temperature experience of each group may be traced by following the appropriate line. For instance, fish entering deep water early in June are indicated by the line broken by a single dot. These fish spend May in water warming from 4°C. to about 12°C. In June they descend to water at 8°C. and they remain in water at this temperature during July. In August they may move up into the upper hypolimnion, where the temperature is about 10°C. In September, due to the descent of the thermocline, they are again forced into water at a temperature of 8°C. and they were still there when investigation ceased for the season. Probably they return to the epilimnion in October, when the temperature has dropped to 12°C. or thereabouts. This group of fish consists in the main of the largest ciscoes, but also contains progressively fewer of the smaller size classes.

The largest ciscoes spend the least time in water above 8°C. The warm water experiences of the other groups vary with the time of their migration both in and out of the hypolimnion. The smaller fish being the last to migrate downwards stay longest in warm water in the spring, but they are quite late in returning to the epilimnion in the autumn. On the other hand, some individuals of the size classes of 25 to 27 cms. migrate moderately early and leave the hypolimnion first of all. These two groups are indicated by lines broken by four and three dots respectively. It is possible

TABLE 14.—Growth of various age groups of lake Nipissing ciscoes during the season of open water.

	Standard length in mm.			
	I	II	III	IV
1933				
June 23-26	140 (42)	190 (10)	220 (4)	260 (2)
July 10-18		200 (14)	224 (113)	243 (29)
July 20-Aug. 3	146 (24)	200 (48)	225 (183)	246 (39)
Aug. 12	156 (13)			
Sept. 30-Oct. 2	141 (1)	202 (15)	230 (25)	245 (24)
Nov. 1-6		211 (8)	237 (22)	249 (12)
1934				
May 2-17			207 (7)	234 (22)
May 18-25		158 (2)		
May 28-June 1		163 (2)	216 (2)	230 (40)
June 22-23	126 (4)	185 (7)	209 (25)	236 (59)
July 16-17	141 (6)	190 (11)	216 (45)	235 (13)
July 24-Aug. 7	140 (1)	193 (16)	222 (13)	
Aug. 7- 9	141 (191)			
Aug. 13-18		195 (9)	221 (61)	238 (167)
Sept. 13-16	142 (3)	196 (3)	223 (17)	240 (31)

0-Group

1931		1932		1933	
Aug. 17	61 (17)	July 27	62 (4)	Aug. 11	59 (10)
Aug. 19	62 (14)	July 31	68 (1)		
Aug. 20	62 (14)	Aug. 4	68 (1)	Sept. 27	78 (6)
Aug. 25	64 (13)	Aug. 7	69 (1)		
Aug. 26	65 (5)	Aug. 9	70 (1)		
		Aug. 13	68 (1)	1934	
		Aug. 22	69 (3)		
		Aug. 31	73 (1)	July 23	55 (6)
				July 26	56 (100)
				Aug. 25	66 (1)
				Sept. 6	75 (1)

that these groups spend, during the whole year, about the same length of time in warm water with the difference that the group of smaller fish stay in the epilimnion longer in the spring, while the larger fish return to it earlier in the late summer.

Some individuals never descend below the thermocline; the possible temperature experience of the hardiest of these is indicated by the broken line. Among this group are the fingerlings.

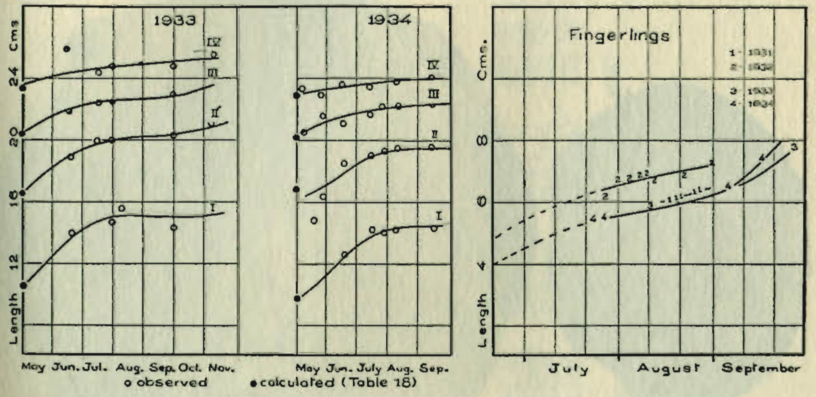


FIGURE 23.—Growth of various age groups of lake Nipissing ciscoes.

Seasonal Growth

Figure 23 illustrates the rate of growth of the age groups 0 to IV during 1933 and 1934. This graph is plotted from the data in table 14.

In all the age groups shown the greatest amount of growth takes place in May, June, and July. This growth is made during the spring period in the epilimnion, when the fish are feeding well.[7] Growth slackens when the fish stop feeding and migrate to the hypolimnion. The fingerling group, which does not migrate, also suffers a depression in growth during August. The reason for this is not clear but it may be connected with the fact that they occupy at this time the

[7]See also Hile (1936), pp. 249-253.

marginal territory of the thermocline. In the fall, growth is recommenced in the age groups 0, I, II, and III. In winter there is no detectable growth. The mid-summer depression in growth is reflected in false annuli laid down in the scales. These checks show most clearly in the fingerling stage by virtue of the broad band subsequently laid down during autumn growth.[8] In figure 24 two scales are shown, taken from two fish in the 1933 year class. The left scale taken

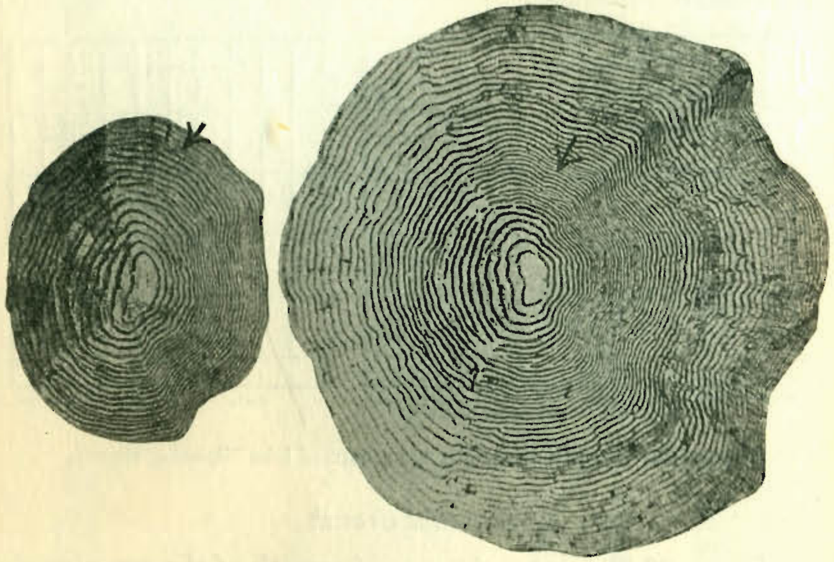


FIGURE 24.—Scales of two ciscoes of the 1933 year class illustrating the summer check. X 20 *ca.*

from a fingerling captured during September, 1933, shows the narrow circuli laid down in August. The right scale was taken from a fish of the same year class captured in 1934; within the first annulus and outside of the "August band" is a region of broad circuli laid down in the fall growth.

In the higher age groups the variation in individual growth rates becomes so great that our samples are inadequate for showing the growing season.

[8]See also Hile (1936), p. 219.

TABLE 15.—The average size in mm. attained by different age groups of lake Nipissing ciscoes during the years 1931, 1932, 1933, and 1934.

Year of capture	AGE II	III	IV	V	VI	VII	VIII	IX	X and over
Males									
1931	213 (2)	229 (13)	240 (38)	252 (21)	264 (9)	282 (6)		428 (1)	
1932	206 (39)	231 (36)	248 (17)	256 (67)	262 (59)	273 (8)	320 (5)		
1933	199 (24)	225 (78)	247 (38)	254 (22)	262 (53)	262 (37)			
1934	195 (9)	218 (23)	239 (61)	255 (23)	260 (9)	276 (11)			390 (2)—10 yrs.
Mean	203	226	241	254	262	274	320		
Females									
1931		237 (4)	243 (24)	251 (8)	260 (6)	302 (1)	280 (3)		
1932	204 (58)	232 (37)	247 (37)	257 (85)	264 (61)	274 (7)	288 (6)	301 (9)	298 (1)—10 yrs.
1933	202 (24)	225 (105)	245 (39)	254 (37)	259 (43)	266 (13)	319 (2)	341 (2)	344 (1)—11 yrs.
1934		225 (38)	238 (96)	254 (30)	268 (15)	267 (14)	278 (5)	404 (1)	281 (1)—11 yrs.
Mean	204	224	242	255	262	269	287	346	

General Growth Curve of the Population

Figure 25 shows the average size attained by different age groups based on samples taken during the years 1931 to 1934. The lengths given are the observed sizes of fish taken in July or August, and thus include some of the growth made during the current year. The graph was obtained by plotting the data contained in table 15.

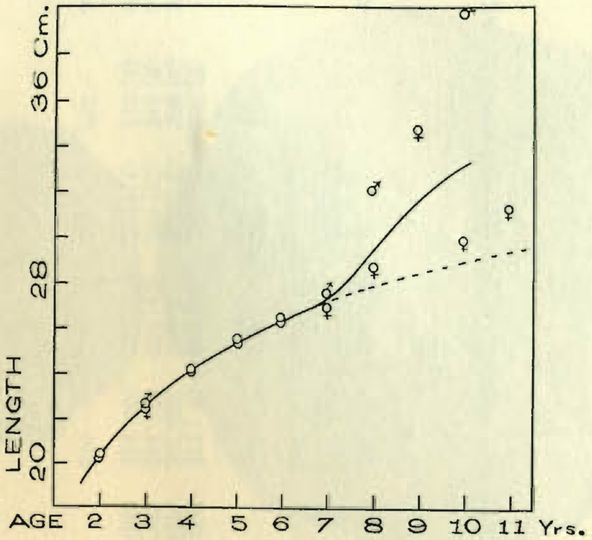


FIGURE 25.—Average length attained by ciscoes of different age groups captured in the hypolimnion in the years 1931-1934 inclusive. Data from table 15.

There seems to be a temporary acceleration in growth in about the eighth year. It is believed that this is significant, although in the higher age groups samples are small and scale reading becomes more unreliable as an index of age. However, if the curve which fits the lower age groups were produced it would tend to approach a constant value considerably below the average length of certain groups of fish, placed together by reason of a similarity in the markings on their scales. Moreover, Pritchard (1931) found a similar growth curve in the bay of Quinte population of *L. artedi*.

This increase in rate of growth is correlated with the increase in the percentage of fish feeding in the hypolimnion, which is found in the older age classes. The following table, compiled from the oblique series of July 23 to 26, 1935, shows this.

TABLE 16.—The percentage of feeding and non-feeding fish in the oblique series at station 4, July 23-26, 1935. Grouped according to age.

	Age									
Males	I	II	III	IV	V	VI	VII	VIII	IX	X
Per cent. feeding.......	28	32	30	43	53	61	68	65	50	100
Per cent. not feeding...	72	68	70	57	47	39	32	35	50	0
Total taken...........	7	54	37	119	99	28	28	23	2	1
Females										
Per cent. feeding.......	50	38	31	43	36	53	65	72	75	100
Per cent. not feeding...	50	62	69	57	64	47	35	28	25	0
Total taken...........	2	57	42	129	148	40	23	29	4	2

Relation between Feeding Activity in the Hypolimnion and Rate of Growth

Not only is there the correlation between the general growth curve and the feeding activity of the population in the hypolimnion which has been discussed in the previous section but there is such a correlation within each age group. This is shown in the following analysis of the sample taken in the July 23 to 26 oblique series at station 4. The results are tabulated in table 17 and are illustrated in figure 26.

In the age groups I to VII, fish classified as feeding are larger than non-feeding fish. The extent of the differences between the groups is irregular, but this is to be expected since in any one group the probable error of this difference is large; for this reason the great difference between the feeding and the non-feeding fish in group I is likely to be due merely to chance. In the age groups VIII and IX the feeding fish are on the average smaller than the non-feeding fish. No non-feeding fish were taken in group X. Parallel differences are found in males and females (table 17). In spite of these irregularities the average difference is significantly greater than zero. No explanation can be offered for the smaller size of the feeding fish in groups VIII and IX. It may be due to random error, although the fact that the

TABLE 17.—Average lengths in mm. of feeding and non-feeding fish in different age groups, taken at station 4, July 23-26, 1935.

	AGE									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Males										
Feeding.......	170 (2)	186 (17)	218 (11)	242 (51)	253 (52)	262 (17)	267 (19)	272 (15)	271 (1)	275 (2)
Non-feeding...	158 (5)	185 (37)	216 (26)	237 (68)	248 (47)	257 (11)	261 (9)	275 (8)	277 (1)	
Females										
Feeding.......	166 (1)	187 (22)	216 (13)	240 (56)	252 (53)	264 (21)	278 (21)	271 (21)	274 (1)	284 (2)
Non-feeding...	156 (1)	186 (35)	214 (29)	235 (73)	237 (95)	259 (15)	259 (8)	274 (8)	278 (3)	
Both sexes										
Feeding.......	169	187	217	241	252	263	273	271	272	280
Non-feeding...	158	185	215	236	241	258	260	274	278	

relation is the same in both sexes argues against this, or to selection brought about by gill nets since 3 inch stretched mesh was the largest used, and the largest fish in these year classes may not have been taken.

This difference in growth rates between feeding and non-feeding fish, which persists through the age classes, lends force to an implication which up until the present could not have been read into the data; namely, that while age is the pre-

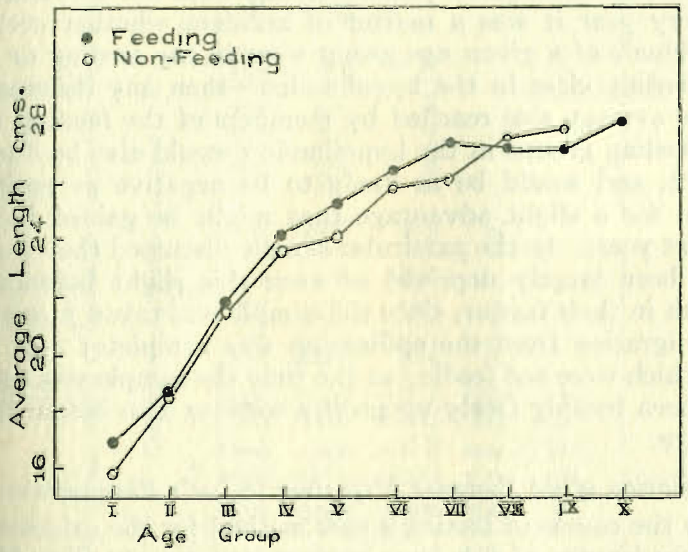


FIGURE 26.—Average lengths of feeding and non-feeding ciscoes in different age groups taken at station 4, July 23-26, 1935.

dominant factor in modifying the migratory activity of an individual, and that after age, sex is next important in this respect, physiological differences in individuals of a given age and sex also play their part in deciding the response to factors bringing about migration. This would mean that not only is there a definite sequence in the migration of the population as a whole, which can be seen by the observation of such attributes of the individual as size and sex, but that within one group of individuals, all within the range of one class with respect to size (age) and sex, there is a definite sequence, In the younger age groups the few individuals which migrate early may be considered to be precocious since they behave like older fish in this respect. Such fish which migrate to the hypolimnion early enough to resume feeding in July, when young, will behave in the same way throughout their subsequent lives. In later years other fish of the same year class will join them in feeding in the hypolimnion, and these, too, when they have once started to feed in the hypolimnion will do so in all subsequent years. If this were not so—that is, if every year it was a matter of accident whether certain individuals of a given age group were in the feeding or the non-feeding class in the hypolimnion—then any differences in the average size reached by members of the feeding and non-feeding groups in the hypolimnion would also be due to chance, and would be as likely to be negative as positive except for a slight advantage that might be gained in the current year. In the particular sample discussed they would have been largely deprived of even this slight balance of growth in their favour, since the sample was taken just after the migration from the epilimnion was complete; thus the fish which were not feeding at the time the sample was taken had been feeding freely up until a week or two before their capture.

Relation of the Summer Migration to Lee's Phenomenon

In the course of testing a new method for the calculation of body lengths of fish from scale measurements (Fry MS.) samples of lake Nipissing ciscoes, taken from the bottom of the hypolimnion in late July and early August in three successive years, were used. Lengths calculated from the scales of the male fish taken in these samples were compared year class by year class.[9] The accompanying table (table 18) summarizes this comparison.

[9]The scale formula used was an adaptation of Huxley's formula for growth partition $y=bx^a$. The logarithmic form of the formula was used with an allowance for the growth of the fish previous to the appearance of the scales. This formula is

log (antero-posterior diameter of scale) $= a \times$log (standard length at capture $-$length at scale formation)$+$log b.

A calculator which solves this formula for different species without the necessity of calculating the constants, is described in a master's thesis (Fry, 1935) deposited in the library of the University of Toronto.

TABLE 18.—Calculated and observed lengths of ciscoes caught on bottom at station 4 in the years 1932, 1933, and 1934 (error given is the P.E. $=0.6745\sigma$M.).

Year class	Year of capture	Age at capture	Calculated length at end of year mm. 1	2	3	4	5	Length at capture mm.
1928	1932	IV	88±0.94 (17)	143±1.2 (17)	195±1.2 (17)	234±2.4 (17)		248±2.3 (17)
	1933	V	89±0.40 (22)	138±1.6 (22)	188±2.4 (22)	221±1.8 (22)	242±1.0 (22)	254±1.1 (22)
1929	1932	III	92±0.61 (36)	154±1.1 (36)	207±1.1 (36)			230±2.0 (37)
	1933	IV	94±0.74 (38)	155±1.3 (38)	205±1.2 (38)	235±1.1 (38)		247±1.5 (38)
	1934	V	93±0.80 (23)	147±1.3 (22)	198±1.8 (21)	230±1.7 (20)	248±2.6 (20)	255±2.2 (23)
1930	1932	II	103±1.2 (25)	163±1.3 (25)				206±0.47 (25)
	1933	III	101±0.51 (78)	153±0.74 (78)	205±0.74 (78)			225±0.15 (78)
	1934	IV	102±0.58 (59)	154±0.67 (59)	205±0.81 (59)	230±0.81 (59)		239±1.0 (61)
1931	1933	II	99±0.94 (24)	164±1.3 (24)				199±0.94 (24)
	1934	III	98±0.62 (22)	158±1.3 (22)	201±1.5 (22)			218±0.47 (23)
1932	1933	I	106±0.45 (14)					144±1.3 (14)
	1934	II	110±1.9 (7)	165±1.9 (7)				195±3.7 (9)
1933	1934	I	96±0.61 (31)					142±1.9 (31)

It will be seen that, no matter what the age of the fish when captured, the calculated values for the length of the fish at the formation of the first annulus, in a given year class, agree within the limits of probable error. Calculations at subsequent annuli show Lee's phenomenon in that the calculated length at a given annulus is usually smaller when calculated from scales of old fish than it is when calculated from younger fish of the same year class. An exception to this rule is found in the groups III and IV where the calculated values in both groups agree.

These discrepancies between lengths calculated from fish of different ages, but of the same year class, may be explained by the relation between migratory and feeding activity, and the rate of growth. In the first year of growth the fingerlings are all in the same locality in the region of the thermocline. Within the limits of our observations these all grow at about the same rate. In their second year certain fish migrate early to the hypolimnion and feed there. Early in their third year these return again to the hypolimnion, together with a few of their year class, which did not feed in the hypolimnion the year before. Our sampling for the scale study was confined to the bottom at 150 feet and the two-year old fish taken belonged largely to this select class, since the feeding fish are concentrated at the bottom in the middle of the summer (figure 21, p. 56). For this reason fish taken at the bottom when two years old show a high average value for the length attained at the time of the formation of the second annulus. The group from which this sample was drawn returned to the bottom of the hypolimnion in late July in subsequent years, but became more and more diluted by the addition of fish that previously had been in the non-feeding group when in the hypolimnion. These other fish grew at a slower rate (figure 26, p. 69), and their calculated lengths brought the average of the group lower and lower except for the length corresponding to the first annulus. The close agreement between III and IV fish must for the present be considered to be due to chance.

The statement regarding the growth of the fingerling group was intentionally qualified. In Nipissing only about one-half of the five-year old fish, the greatest age of fish used in this comparison of calculated lengths, are in the feeding group, and perhaps if reliable averages could be calculated from higher age groups, Lee's phenomenon might also be detected at the first annulus. In lakes where the ciscoes live under conditions that are more severe than they are in Nipissing, this might be seen, since a differential mortality might remove the group of ciscoes in these lakes analogous to the "feeding" group present in the hypolimnion of lake Nipissing. This, of course, would shift the average much more quickly.

Some evidence of differential distribution according to size of members of a year class even in the first year, can be found by comparing lengths calculated from fish captured in shallow water with those calculated from fish of the same age captured in 150 feet of water (table 19).

TABLE 19.—Comparison of calculated lengths at the first annulus in ciscoes of the same year classes captured in deep and shallow water in 1934. (error given is P.E. $=0.6745\ \sigma$ M).

Year class	Shallow water	Deep water	Difference
1930	98±0.71 (27)	102±0.58 (59)	4±0.97
1931	94±0.41 (24)	98±0.62 (22)	4±0.82

A difference may also be seen in a comparison of the actual diameters of the scales (table 20).

TABLE 20.—Scale diameters in shallow and deep water catches, 1934.

Annulus	Shallow water Diam. mm.	Deep water Diam. mm.
1	3.85	4.02
2	4.97	5.58
3	5.75	6.44
4	6.55	7.30
5	6.30	7.78
6	6.77	8.36
7	7.40	8.43

A Possible Relation between the Summer Migration and the Development of the Germ Cells

It is conceivable that the length of the warm water experience in the fall may affect the rate of development of the gametes, and thus, provided that the water cools to spawning temperatures quickly enough, influence the time at which certain fish spawn, since the fish which leave the hypolimnion last may not be ripe until after the earlier migrants are already spawning. This, however, is a suggestion which must be cautiously advanced, since it has been impossible to test this hypothesis directly. It may be seen, by reference to figure 27, that the eggs in the ovaries of Nipissing ciscoes grow rapidly in the fall and may not in all

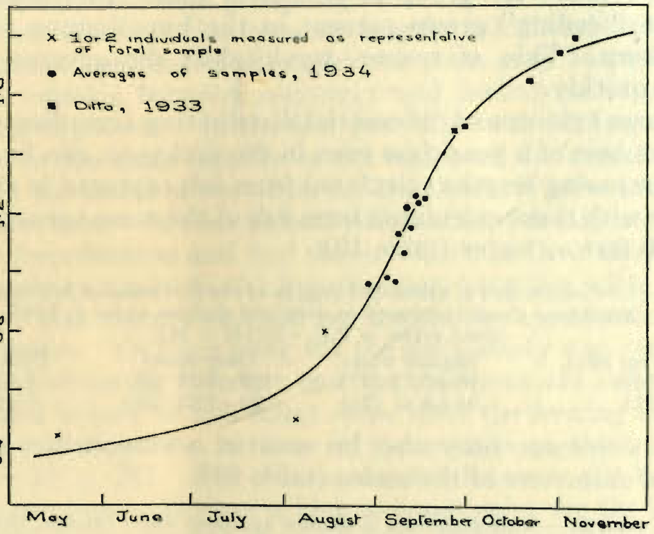


FIGURE 27.—Rate of growth of the eggs in the ovary of the lake Nipissing cisco.

cases have completed growth before the water temperature has dropped to 4°C., the temperature at which ciscoes are considered to spawn (Cahn, 1927).

Since practical difficulties prevented a study of the spawning in lake Nipissing, an attempt was made to discover a trend in size in spawning ciscoes in the eastern end of lake Ontario during November, 1934, but the results were inconclusive. Three samples were taken on November 22, 26, and 30, respectively, from schools near the south-western end

of Amherst island. These fish were captured in gill nets, fished commercially by Mr. S. Thompson of Pleasant Point. From his catches females were selected; these were measured and on the basis of an examination of the gonads the fish were classified in the following four categories.

(a) **Spent.** Few or no mature ova within the ovarian membrane, ovigerous stroma contracted.

(b) **Partly Spent.** Some eggs within the posterior part of the ovarian membrane, ovigerous stroma contracted.

(c) **Ripe.** Ovarian membrane filled with mature eggs, ovigerous stroma contracted.

(d) **Not Ripe.** Ovaries filled with mature eggs, ovigerous stroma expanded.

Two things were found in these samples. Firstly, all fish were not spawning at the same time, for in the last catch there was still a number of unripe fish. The proportions of fish in different stages taken in the three samples are given in table 21. Secondly, the fish in the sample taken on November 26 had an average length which was significantly greater than that of the sample taken November 22. However, the sample of November 30 had the lowest average length of all, but this difference was not significant. The only conclusions that may be drawn from these results are that all ciscoes are not ready to spawn at the same time, and that spawning schools in the same locality may differ in their size compositions. There is no evidence either for or against a temporal succession that is correlated with size, and hence with the fall migration from the hypolimnion.

TABLE 21.—Condition of the ovaries in three samples of ciscoes taken at the spawning season in lake Ontario in 1934.

Date	Number taken	Per cent. spent	Per cent. partly spent	Per cent. ripe	Per cent. not ripe
Nov. 22	140	18	31	32	20
Nov. 26	168	25	39	29	7
Nov. 30	71	22	21	32	24

SUMMARY

1. In lake Nipissing there is a general migration of the cisco population from shallow to deep water in late spring and early summer. This movement takes most of those members of the population which participate in it below the thermocline. They remain in the hypolimnion for some time, scattering downwards until evenly distributed throughout its extent. During late August and September they rise from the bottom, concentrate under the thermocline, and most of them pass through the thermocline to return to shallower water before the fall turnover.

2. The downward movement of the fish is correlated with rising temperatures in the epilimnion. Their continued descent when they have passed through the thermocline seems to be a scattering comparable to the diffusion of molecules. The subsequent ascent from the bottom in late summer is correlated with decreasing concentrations of dissolved oxygen and increasing amounts of carbon dioxide in solution in the bottom water. A consideration of the actual concentrations of these substances in light of certain experiments indicates that it is probably the increase in carbon dioxide which is the more important factor affecting this movement. The concentration of fish immediately below the thermocline at this season is considered the result of the ascending population's avoidance of the warm water of the epilimnion when suddenly subjected to it after experiencing the cool, even-temperatured waters of the hypolimnion. The final evacuation of the hypolimnion is due to the destruction of this balance between the opposing effects on the ciscoes of the warm water above and the unfavourable concentrations of dissolved gases below. This destruction is brought about by further cooling of the epilimnion, and a further increase of the concentration of carbon dioxide and the decrease of dissolved oxygen in the hypolimnion.

3. The migration to the hypolimnion is not a simple mass movement of the whole population in which the increase of population in the hypolimnion is due to the chance descent of schools below the thermocline. It is rather an orderly succession of certain groups of individuals which migrate in the order of their size and sex. The downward succession is, first, the largest males, followed by large males and the largest females; these in turn are followed by smaller males and large females and so on. The two youngest age groups are the last to move downwards, and their migration is never as complete as that of the older groups.

The upward movement is more complicated. Quite large, but by no means the largest fish, pierce the thermocline earliest. The order of leaving, subsequent to this movement, involves fish both above and below the intermediate sized class which left first. The smallest fish leave late and the last of all to go are the largest males.

4. These movements have been explained as follows. The succession observed in the downward movement, in which the largest males go first and small females last, appears to mean that the largest males have the lowest upper temperature threshold. The fish with low upper temperature thresholds are presumed to have also a low tolerance towards high concentrations of carbon dioxide. The complex order of return to the epilimnion depends on the quantitative balance between these two intolerances.

5. The extent of migration may vary from year to year. In four of the seven years in which the observations were made, the fish left shallow water by about the middle of July. In the remaining three, migration was still incomplete by the end of that month. This fluctuation of migratory activity is correlated with the average July temperature of the water less than thirty feet deep.

6. Profound changes in the feeding activity of the population are correlated with the summer migration. Fish apparently stop feeding just prior to migrating below the thermocline and do not begin feeding again immediately. The length of time during which they do not feed varies with the time at which they migrated. Fish migrating early may begin feeding about a week after entering the hypolimnion. The last migrants may not feed for a period of six weeks or even longer.

When the fish first leave the hypolimnion in the autumn they again stop feeding for an undetermined period of time.

7. With respect to the summer migration the cisco population of lake Nipissing behaves as a single species.

8. There is a correlation between the summer migration and the rate of growth. Most of the growth of the population is made during the spring period in the epilimnion, the greater part of the population stops growing during the midsummer period, but growth recommences in the younger age classes in the autumn.

9. The migration to the hypolimnion complicates the annual cycle of temperature experienced by the cisco. Most fish spend a spring and a fall period in quite warm water separated by a midsummer period in cool water. Different groups of the population experience these two periods in different degrees, depending upon the times at which they migrate.

10. Certain individuals found to be feeding in the hypolimnion in July grow more quickly than individuals of the same age and sex which are not feeding in the hypolimnion at this time. The proportion of the members of a year class which feed in the hypolimnion in July increases as the year class becomes older. Correlated with this increase in feeding activity there is an acceleration in growth in the higher age groups.

11. There are individual differences in the age at which ciscoes descend to the hypolimnion early enough to feed there in July. Some fish feed there in their second season, others not until later than their seventh. Evidence is presented that suggests that when once a fish has fed in the hypolimnion it always does so in subsequent years.

12. The occurrence of Lee's phenomenon in calculations of the lengths of lake Nipissing ciscoes from scale measurements, has been explained on the basis of individual differences in migratory activity and the correlation of these with the individual's rate of growth.

13. A possible relation between the summer migration and the time of spawning has been suggested.

DISCUSSION

The broad problem, towards the solution of which this study has been intended to contribute, is the problem of raciation in ciscoes. The immediate aim has been towards the solution of the following problems. Does the behaviour of the lake Nipissing population give any indication that selection could have any effect in altering the genetic constitution of an isolated population of ciscoes? What possibilities are there of the environment moulding the body form of ciscoes?

The first of these questions may be answered in the affirmative. Certain members of the population are more limited in their movements, and more especially in their feeding activities by factors in the environment. This differential reaction indicates that selection may take place, since all individuals are not afforded an equal opportunity to move and feed. In some lakes this restriction may be so severe as to bring about the death of certain individuals (Hile, 1936; Cahn, 1927).

There is also considerable opportunity for the environment to exert a moulding influence. Since the thermocline divides the lake into two regions, there may be wide fluctuations in the conditions under which the ciscoes live in lake Nipissing without the population being affected by selection through fatalities. Temperature conditions in the lake fluctuate annually, but the important thing is that the proportions of the summer spent by the ciscoes above and below the thermocline vary from year to year. Thus in one year they may stay in the epilimnion during the greater part of the summer; in another they may migrate to the hypolimnion early in July. Consequently slight differences in epilimnial temperatures may have a very great effect on the temperature experience of the population. These fluctuations in temperature experience may affect growth rate and spawning time and through these, and by other means as well, the form of the ciscoes may be affected.

A study of the behaviour of the ciscoes suggests, then, the possibility of both a selection and a moulding. The difficulty lies in assessing the relative importance of each of these processes on the fish. Different sections of the population grow under different conditions which gives rise to a situation that affords an opportunity for the environment to act on them in different ways, but the reactions of the individuals which place them in these conditions may be due to their heredity. Even if a perfect correlation could be found between the characters of individuals and the environment to which they are subjected it would not be evidence that the environment alone was responsible for these differences. The reactions of the individual which resulted in bringing it or its offspring into contact with that environment, must be taken into account. The matter becomes further complicated when the genetic differences between individuals are of such a nature as to determine the rate at which they change their migratory activity.

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APPENDIX I

DISTRIBUTION OF FISH IN OBLIQUE CATCHES

The following tables contain the actual numbers of fish taken in the vertical samples. At station 3 each 15 foot stratum was fished by three 50 yard nets including 1½, 2¼ or 2½, and 3 or 3¼ inch stretched mesh. At station 4 this same gang of nets was used until July 17. To make a series the gang had to be fished three times with the order of the nets changed. Since there were only nine nets and the water was 150 feet deep, the bottom 30 feet were fished by one net, making 25 yards to a 15 foot stratum here. After July 17 gangs 2 and 2-A were used. These gangs were made up of only three 50 yard nets, gang 2 consisting of 1½, 2¼, and 3 inch mesh, gang 2-A having the same mesh except that 2 inch was substituted for 1½ inch, since the 1934 year class seemed to be very poor and it was felt that of the young fish it was better to sample the large 1933 year class. With this three net gang 15 foot strata from 90 to 150 feet were fished with quarter nets; similar strata from surface to 90 feet were fished by 1/3 of a 50 yard net.

In the tables the catches are analysed into size, depth, sex, and the state of the stomach (E stomach empty, F stomach containing at least a trace of food).

In comparing these catches graphically, the actual catches have been multiplied by factors. The standard taken for figures 7 and 14 is the number of fish taken per 15 foot stratum by 50 yard nets fished for twelve hours. The catches at station 3 need no correction. The catches at station 4 before July 16 require only a doubling of the number of fish taken from 120 to 150 feet. The July 16-17 catch was only 1/3 of a series and the numbers plotted are an estimate of a complete series. Later catches at station 4 require the numbers taken above 90 feet to be multiplied by three, below 90 feet by four and to be increased further by a factor to bring the length of fishing up to 12 hours. In figure 21 the standard is 50 yard nets for twelve hours for the first three series. For the late series 16 2/3 yard nets are taken as the standard.

Other minor corrections were made in preparing figures 7 and 14. Fish over 20 cm. taken in the smallest mesh were omitted but they have been included in the table.

TABLE 7.—Numbers of ciscoes taken in oblique series at station 3, 1935.

Date	Duration of set hours	Gear	Fish caught 20 cm. E	20 cm. F	20-25 cm. E	20-25 cm. F	25 cm. E	25 cm. F	Depth feet
June 13	12	Gang 1	0	0	1	3	1	6	0-15
			0	2	0	8	0	13	15-30
			0	7	0	30	2	20	30-bot.
July 10	12	Gang 1	2	0	0	34	0	20	0-15
			0	7	0	32	2	10	15-30
			0	4	4	28	4	12	30-bot.
July 10	day	Gang 1	0	0	0	0	0	1	0-15
			0	0	2	4	0	1	15-30
			0	0	2	17	0	15	30-bot.
August 12	12	Gang 1	no ciscoes taken at any depth						

TABLE 8.—Ciscoes taken in oblique series at station 4, 1935.

June 10-13, Gang 1, Set 12 hours

Depth feet	Small				Medium				Large			
	♂		♀		♂		♀		♂		♀	
	E	F	E	F	E	F	E	F	E	F	E	F
0- 15	0	0	0	1	0	2	1	3	0	5	2	6
15- 30	0	2	0	2	2	1	2	4	1	2	2	5
30- 45	0	0	0	1	2	2	0	3	1	3	4	3
45- 60	0	0	0	0	0	1	0	1	3	3	1	6
60- 75	0	0	0	0	0	1	1	0	1	0	0	4
75- 90	0	0	0	0	0	1	0	0	2	5	0	1
90-105	0	0	0	0	0	0	0	0	0	2	0	0
105-120	0	0	0	0	0	0	0	0	0	1	0	0
120-150	0	0	0	0	0	0	0	0	1	0	1	0

June 20-23, Gang 1, Set 12 hours

Depth feet	Small				Medium				Large			
	♂		♀		♂		♀		♂		♀	
	E	F	E	F	E	F	E	F	E	F	E	F
0- 15	0	3	0	4	1	2	0	0	0	0	1	3
15- 30	0	1	0	1	1	2	0	0	1	1	4	0
30- 45	0	0	1	1	1	0	1	2	5	2	1	0
45- 60	0	1	0	8	2	0	0	2	10	3	13	7
60- 75	0	0	0	0	0	0	2	1	11	3	15	3
75- 90	0	0	0	1	1	0	0	0	2	0	7	1
90-105	0	0	0	0	1	0	0	1	11	11	7	3
105-120	0	0	0	0	0	1	0	0	2	1	2	2
120-150	0	0	0	0	0	0	1	0	2	2	0	1

July 3-6, Gang 1, Set 12 hours

Depth feet	Small				Medium				Large			
	♂		♀		♂		♀		♂		♀	
	E	F	E	F	E	F	E	F	E	F	E	F
0- 15	0	1	0	0	1	2	0	2	0	1	0	1
15- 30	0	0	0	0	0	2	1	1	0	0	2	0
30- 45	2	5	0	4	1	1	0	0	2	0	2	0
45- 60	0	1	0	0	1	3	0	0	7	2	5	3
60- 75	3	2	4	7	1	1	1	0	5	4	2	7
75- 90	0	0	0	0	1	2	1	3	4	10	9	4
90-105	0	0	0	0	0	1	0	0	1	6	0	4
105-120	0	0	0	0	0	1	0	0	0	6	1	7
120-150	0	0	0	0	0	1	0	0	0	7	1	6

July 16-17, Gang 1, Set one night only

Depth feet	Mesh ins.	Small				Medium				Large				Not exam-ined
		♂		♀		♂		♀		♂		♀		
		E	F	E	F	E	F	E	F	E	F	E	F	
0- 15	3	0	0	0	0	4	6	2	4	1	2	4	5	0
15- 30	2½	1	2	2	0	6	5	9	1	2	1	2	0	0
30- 45	1½	1	0	1	0	0	0	0	1	0	0	0	0	0
45- 60	3	0	0	0	0	9	4	17	4	23	3	14	3	50
60- 75	2½	0	0	2	0	32	2	20	3	12	2	23	2	96
75- 90	1½	4	3	7	1	1	0	1	0	0	0	0	0	0
90-105	3¼	0	0	0	0	10	6	7	2	11	16	10	15	87
105-120	2¼	1	0	2	0	11	7	7	3	3	7	3	7	0
120-150	1½	0	0	0	0	0	0	1	0	0	0	0	0	0

July 23-26, Gang 2, Set 12 hours

Depth feet	Small				Medium				Large			
	♂		♀		♂		♀		♂		♀	
	E	F	E	F	E	F	E	F	E	F	E	F
0- 15	0	0	0	0	0	1	2	1	2	1	3	2
15- 30	1	0	0	0	4	2	2	0	2	1	3	1
30- 45	1	0	0	0	4	3	4	5	3	1	5	2
45- 60	1	0	4	3	12	4	7	6	4	4	6	3
60- 75	9	3	9	2	19	4	27	3	9	7	14	8
75- 90	17	1	14	5	54	8	57	4	19	10	28	3
90-105	17	3	9	2	20	8	28	7	27	16	20	9
105-120	5	0	6	1	15	3	19	8	2	15	14	21
120-135	1	2	2	1	6	6	12	12	7	13	6	21
135-150	1	0	3	0	8	14	7	11	2	22	5	23

August 15-20, Gang 2-A, Set 8 hours

Depth feet	Small				Medium				Large			
	♂		♀		♂		♀		♂		♀	
	E	F	E	F	E	F	E	F	E	F	E	F
0- 15	0	0	1	0	0	0	0	1	1	0	1	0
15- 30	0	0	1	0	2	0	1	1	0	0	0	3
30- 45	0	1	2	0	1	1	2	1	0	0	1	2
45- 60	5	0	0	1	3	1	8	1	1	2	3	3
60- 75	7	0	5	4	6	0	12	0	7	1	6	1
75- 90	10	1	8	2	21	5	36	3	19	3	20	3
90-105	5	1	5	0	26	2	20	2	13	3	18	6
105-120	14	0	12	1	26	4	34	7	13	0	16	6
120-135	15	2	15	3	19	4	32	5	15	8	14	8
135-150	9	1	12	2	17	9	21	9	9	7	5	13

September 4-9, Gang 2-A, Set 9 hours

Depth feet	Small ♂ E	Small ♂ F	Small ♀ E	Small ♀ F	Medium ♂ E	Medium ♂ F	Medium ♀ E	Medium ♀ F	Large ♂ E	Large ♂ F	Large ♀ E	Large ♀ F
0- 15	0	1	1	0	2	1	2	0	0	0	0	0
15- 30	0	0	1	0	1	0	0	1	3	0	0	0
30- 45	0	0	1	0	1	1	6	1	0	0	3	0
45- 60	1	0	1	1	2	1	5	1	3	1	3	3
60- 75	0	0	1	1	2	4	2	2	2	4	1	1
75- 90	1	4	3	10	5	10	10	23	1	9	8	16
90-105	16	10	11	6	35	21	43	31	12	7	21	16
105-120	20	11	17	7	41	22	33	19	5	10	14	6
120-135	15	9	9	7	17	15	19	6	10	11	13	11
135-150	4	4	1	1	8	7	2	4	3	1	1	0

September 18-21, Gang 2-A, Set 12 hours

Depth feet	Small ♂ E	Small ♂ F	Small ♀ E	Small ♀ F	Medium ♂ E	Medium ♂ F	Medium ♀ E	Medium ♀ F	Large ♂ E	Large ♂ F	Large ♀ E	Large ♀ F
0- 15	0	0	1	1	0	0	1	0	1	0	1	0
15- 30	1	0	0	0	2	0	0	0	2	2	2	1
30- 45	0	0	0	0	4	0	1	1	3	1	2	2
45- 60	6	1	3	0	6	0	10	0	6	0	8	0
60- 75	4	0	5	0	5	1	4	0	8	0	3	0
75- 90	2	0	5	0	1	0	5	0	9	3	5	5
90-105	5	1	1	0	3	1	2	1	8	0	4	3
105-120	2	0	1	0	7	3	2	4	10	9	3	11
120-135	1	1	2	2	8	5	6	5	9	7	3	5
135-150	0	0	0	0	1	2	2	1	1	6	2	8

TABLE 9.—Size composition of catches of ciscoes taken in oblique series at station 4.

Length class cm.	June 10-13 ♂ E	♂ F	♀ E	♀ F	June 20-23 ♂ E	♂ F	♀ E	♀ F	July 3-6 ♂ E	♂ F	♀ E	♀ F
20.5	0	0	0	0	0	0	0	0	0	1	1	0
21.5	1	0	1	0	0	0	0	1	0	1	0	0
22.5	1	1	1	5	0	0	1	0	0	1	0	0
23.5	0	3	0	2	3	1	0	2	1	2	0	2
24.5	2	3	2	4	6	4	3	3	5	7	3	3
25.5	1	4	1	7	6	3	10	1	7	8	5	3
26.5	3	8	5	8	11	3	14	4	3	6	4	6
27.5	2	6	4	2	13	8	15	6	2	5	8	6
over 28.0	3	4	0	8	12	9	11	9	7	16	5	17

Length class cm.	July 16-17 ♂ E	♂ F	♀ E	♀ F	July 20-23 ♂ E	♂ F	♀ E	♀ F	August 15-20 ♂ E	♂ F	♀ E	♀ F
20.5	3	2	1	0	6	1	8	1	11	1	11	4
21.5	7	3	2	0	11	3	17	5	13	2	17	2
22.5	11	5	7	3	20	6	36	8	16	1	28	2
23.5	26	7	17	8	45	12	46	15	36	14	49	10
24.5	28	11	36	7	60	32	57	32	47	7	62	12
25.5	23	11	30	14	41	31	54	37	38	11	40	19
26.5	15	14	8	4	18	35	24	27	20	9	28	14
27.5	10	9	6	10	12	19	16	20	10	2	9	7
over 28.0	4	6	7	4	7	5	9	10	7	3	6	4

Length class cm.	September 4-9 ♂ E	♂ F	♀ E	♀ F	September 18-21 ♂ E	♂ F	♀ E	♀ F
20.5	14	9	6	7	1	0	1	1
21.5	15	14	26	19	4	3	3	0
22.5	25	20	23	14	8	2	7	1
23.5	30	25	34	25	11	3	5	6
24.5	25	16	38	24	14	5	15	4
25.5	19	18	28	23	23	5	14	8
26.5	14	10	16	17	12	10	12	13
27.5	3	11	9	7	16	7	5	8
over 28.0	1	2	5	2	5	5	4	6

APPENDIX II

Statistical Procedures

In the course of this investigation the practice has been to apply tests to determine the statistical significance of certain observations. The various formulae, which have been omitted from the text for the sake of brevity, are gathered together here.

(*a*) *Standard Deviation of the Mean*

$$\sigma M. = \pm \sqrt{\frac{\Sigma v^2}{n(n-1)}}$$

where $v = x - \bar{x}$

and n = the number of variates.

(Tuttle and Satterley, 1925)

(*b*) *The* χ^2 *Test*

$$\chi^2 = S_s \frac{N_1 . N_2 \left(\frac{{}_1n_s}{N_1} - \frac{{}_2n_s}{N_2}\right)^2}{{}_1n_s + {}_2n_s}$$

where N_1 and N_2 are the two totals.

${}_1n_s$ and ${}_2n_s$ are the frequencies in one corresponding class in the two distributions.

and S_s is the summation over all groups.

(Tippet, 1931, p. 72)

(*c*) *Standard Error of Sex Ratios*

$$\sigma P = \pm \sqrt{\frac{P - P^2}{n}}$$

where P = the fraction of the whole sample that consists of individuals of one sex.

(Tippet, 1931, p. 57)

(*d*) *Significance of Means of Small Samples*

The significance of the difference between the average size of feeding and non-feeding fish was calculated by finding the average difference in size between these two groups in all age classes as a percentage, and calculating the significance of this difference from zero, by finding the value of t,

such that $t = \frac{1}{n^1} \Sigma x \sqrt{\frac{n^1(n^1 - 1)}{\Sigma(x - \bar{x})^2}}$

where x = the percentage difference in length between feeding and non-feeding fish.

and n^1 = the number of age groups compared.

The significance of t may be found in Fisher's Table. For an example of this procedure, see Fisher (1928), p. 105.