POPULATION FLUCTUATION OF THE CISCO IN BIRCH LAKE, MICHIGAN

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A STUDY OF THE POPULATION FLUCTUATIONS OF THE CISCO, *COREGONUS ARTEDI* (LE SUEUR) IN BIRCH LAKE, CASS COUNTY, MICHIGAN, WITH SPECIAL REFERENCE TO THE GILL-NET SPORT FISHERY

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INTRODUCTION

The shallowwater cisco, *Coregonus artedi* (LeSueur) is found in many lakes of the Great Lakes region and the upper Mississippi River system and northward through the southern drainages of Hudson Bay (Hubbs and Lagler, 1958). This fish formerly was quite common in the Great Lakes themselves, and also is found in many deeper inland lakes where conditions are suitable for its survival. In the Great Lakes, where it is called the "lake herring," the vertical distribution of the cisco is somewhat intermediate to that of the warmwater fish and the deepwater members of the whitefish family. However, in inland lakes it is a deepwater fish and inhabits the deepest and coldest water available, at least during times of the year when limnological conditions are favorable. The cisco is a pelagic spawner. In late autumn the adults move out of the deeper water and onto shallow shoal areas where, apparently mostly at night, the eggs are broadcast over the bottom. The eggs hatch the next spring and the larvae begin to feed on plankton, which they will do for the rest of their lives. The species is relatively short-lived and individuals normally survive about 5 or 6 years.

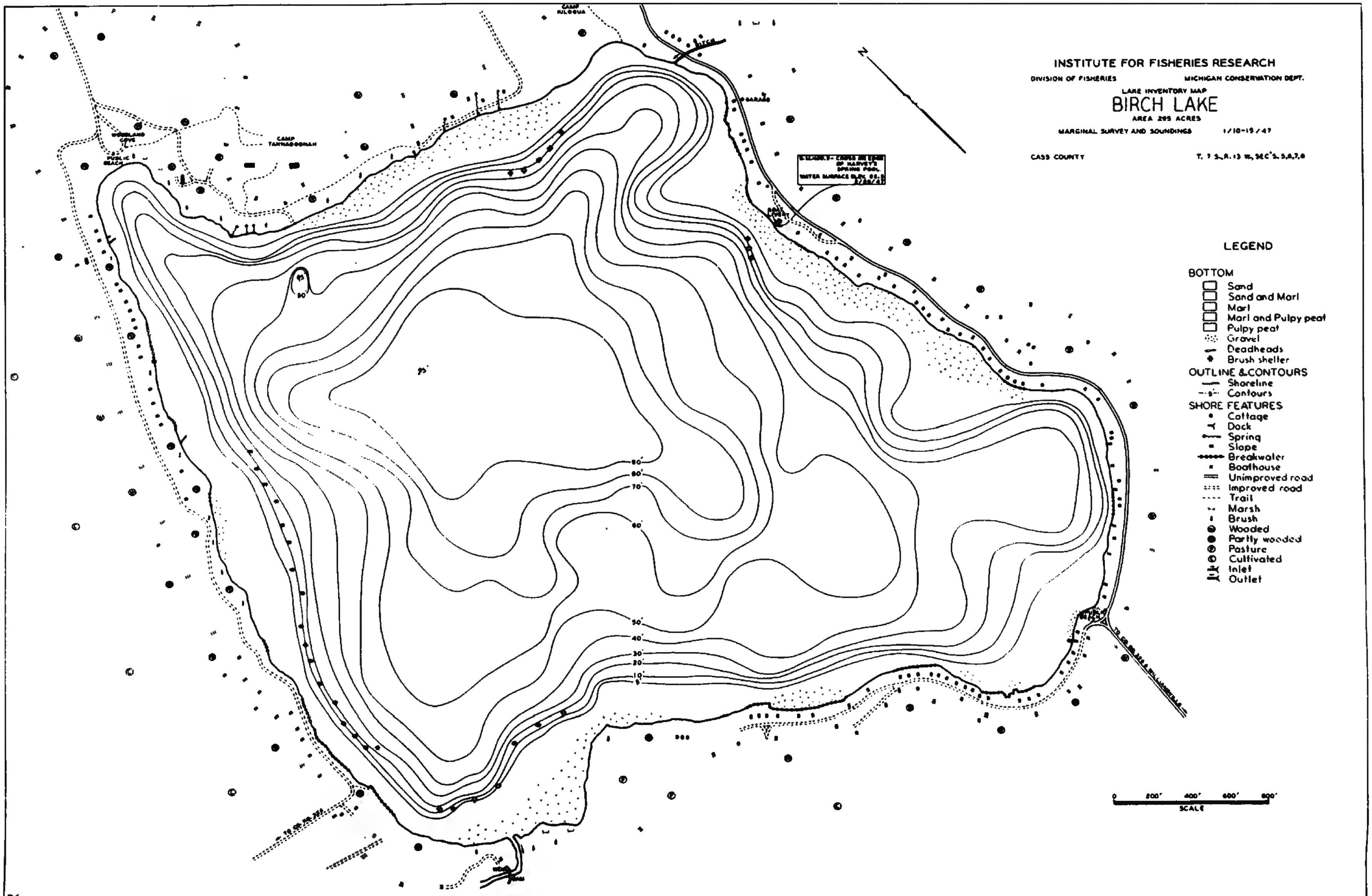
Morphologically, *Coregonus artedi* is a very plastic species, as are many members of the whitefish family. Meristic characters and body proportions vary greatly for the species from lake to lake and even from year to year within the same body of water. Variation is so great and widespread that a large number of populations, 24 to be exact, were recognized as distinct subspecies by Dr. Walter Koelz, who did much of the early taxonomic work with the coregonids in the Great Lakes region (Koelz, 1929, 1931). Later, Hile (1937) found that the differences upon which the subspecific separations were based were too narrow, in view of the wide natural variation, and concluded that larger samples of ciscoes would have to be studied before the numerous subspecies could be justified. The present study does not include taxonomy of the cisco because sufficient material was not available. It is felt that the inclusion of this population in the typical inland deep-bodied form is acceptable for the purposes of this study.

Many authors have studied the sometimes violent fluctuations which the cisco populations of the Great Lakes have shown throughout the history of the fisheries there (Scott, 1951; Pritchard, 1931; Smith, 1956; Van Oosten, 1930). Others mention similar, though apparently less violent, changes of cisco populations in inland lakes (Carlander, 1943; Hile, 1936). This study of an inland cisco population deals with such fluctuations over a period of 25 years, with a few minor gaps during this time. The study suffers somewhat because the quality and quantity of data varies considerably over this extended period. Nevertheless, the study is justified simply because it apparently is the first investigation of the cisco which contains some population, growth, and life history data throughout the entire period of population change.

FEATURES OF BIRCH LAKE

Birch Lake, Cass County, Michigan, is located in the southeastern corner of the state, only 8 miles from the Indiana border. It is spring-fed, has an area of 295 acres with a maximum depth of about 95 feet, and has an outlet into the St. Joseph River drainage. The surrounding country is rolling, wooded upland. Much of the lake is over 50 feet deep, so it contains a large volume of cold, oxygenated water suitable for the survival of the cisco, even during summer stratification (Fig. 1). Hooper (1956) characterizes this type of lake by an abrupt slope at the drop-off between 5 and 20 feet, the small volume of the epilimnion in comparison with the hypolimnion, littoral soils of marl, a small percentage of the bottom supporting submerged, rooted aquatic plants, and water with high methyl orange alkalinity, conductivity, and calcium content. The limited shallow areas support populations of warmwater fish such as yellow perch, largemouth and smallmouth black bass, suckers, bullheads, gar, bluegills, and other panfish. Due to its geographic location, natural beauty, and unusual depth, Birch Lake has long been an important lake for public recreation in Michigan.

Figure 1.--Map of Birch Lake, Cass County, Michigan.



BIRCH LAKE Cass County T. 7 S., R. 13 W., Secs. 5,6,7,8

Figure 1

HISTORY OF FISHERY

Even though Birch Lake is a two-story lake, the warmwater fish production has always been low and coldwater species have dominated the local fishery. For many years the lake has been one of a number throughout southern Michigan open to a sport fishery in which gill nets may be used to take ciscoes during their fall spawning migration onto the shallow shoal areas. Presently the law sets the season from November 15 to December 10, inclusive. Gill nets must be no more than 165 feet in length, and shall have a mesh size of not less than 2 inches or more than 4 inches extension measure. Each fisherman is limited to one net and may fish it only between sunset and sunrise. The laws in the past have varied slightly as to the open season and time of set, but have remained essentially the same since the beginning of the netting. The cisco has very fat flesh and therefore is not considered as good a food fish as the lake whitefish, *Coregonus clupeaformis*. However, the cisco is excellent smoked and the local people in the Cass County area extensively fish many of the 16 lakes open to the gill-net sport fishery.

Due to its morphometry, Birch Lake has been thought to be a first-class trout lake. Records show that as early as 1907 lake trout were stocked in the lake. In 1938 an extensive program of rainbow trout stocking was initiated, and that fall there were reports that the cisco netters were taking large numbers of rainbow trout in their gill nets. This led to an investigation the following year by the Institute for Fisheries Research of the Michigan Department of Conservation which disclosed that some rainbow trout were being taken (Bowditch[1]). More significantly, it began a series of collections of data on the spawning population of the cisco which has continued, at least intermittently, to the present time. An estimated 20,750 ciscoes were taken during the 17-day netting season of 1939.

Birch Lake was closed in 1940 to gill netting of ciscoes until further research was completed to determine the harm done to any other game fish, especially trout, by the netting. Nothing was done for the next 3 years and the lake remained closed. Then, in 1943 an extensive experimental netting project was carried out (Washburn[2]). This and other studies of the Birch Lake cisco will be referred to later, so it is not necessary to summarize the findings now. As a result of this study it was recommended that the lake be re-opened to the taking of ciscoes under special regulations. A maximum harvest limit of 20,000 ciscoes, the approximate number netted in 1939, was placed on the lake. Fishing hours were restricted to between 5:00 PM and 11:00 PM and netting was allowed only within depths of 8 to 25 feet, because it was

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1 Bowditch, Harold. 1939. Cisco netting on Birch Lake, Cass County during the season of 1939. Michigan Department of Conservation, Institute for Fisheries Research, Rept. No. 570, 3 p. [Typewritten]

2 Washburn, George N. 1944. Experimental gill netting in Birch Lake, Cass County, Michigan. Michigan Department of Conservation, Institute for Fisheries Research, Rept. No. 948, 33 p. [Typewritten]

found that during these hours and at these depths the least number of other species were taken. The lake has continued to be open to cisco netting to the present time.

The total catch of ciscoes through 1950 is given in Table 1. It can be seen that a tremendous decline in the catch occurred. Table 2 shows that the fishing pressure exhibited a similar trend. Every fisherman was required to obtain a permit each night before setting his net. It appears that a large percentage of the fishermen continued to net the lake some, but with the reduction in the population simply did not fish as many nights. However, this was not the case, at least not until the fall of 1950. It can be seen from Table 2 that the average number of nights fished per fisherman did not drop significantly through 1949. So the number of fishermen actually did decline at about the same rate as the catch. Table 3, which gives the individual fishermen's catch of ciscoes shows, however, that the drop in catch was due to a decline in population rather than to a reduction in fishing pressure. A progressive decline in the number of fishermen taking large numbers of ciscoes is evident.

Why were the fishermen willing to quickly abandon the lake? Instead of a large number decreasing their effort on the lake, most discontinued fishing Birch Lake completely, while some remained and continued fishing at the same intensity. The reason is that there are 15 other lakes open to cisco netting in Cass County alone, and in the years following an apparent decline of the cisco population the

Table 1.--Catch of ciscoes in Birch Lake by years

Year	Number of ciscoes
1939	20,750
1943	2,108[a]
1944	18,137
1945	11,361
1946	3,600
1947	1,015
1948	417
1949	178
1950	37

[a] Based on experimental netting only. There was no open season in 1943.

Table 2.--Fishing pressure of gill-net fishermen in

Birch Lake, 1939-1950

Year	Number of permits	Number of fishermen	Average nights fished per fisherman
1939	766	-	-
1944	582	105	5.5
1945	743	126	5.9
1946	651	121	5.4
1947	263	68	3.9
1948	280	57	4.9
1949	172	33	5.2
1950	43	20	2.2

Table 3.--Frequency distribution of fishermen in terms of annual catch of ciscoes, 1944-1950

Number caught	Corresponding number of fishermen						
	1944	1945	1946	1947	1948	1949	1950
0	3	7	14	11	16	4	9
1-50	32	51	80	49	41	29	11
51-100	20	32	18	8	-	-	-
101-150	13	15	7	-	-	-	-
151-200	7	5	2	-	-	-	-
201-250	6	4	-	-	-	-	-
251-300	5	6	-	-	-	-	-
301-350	5	3	-	-	-	-	-
351-400	5	-	-	-	-	-	-
451-500	3	1	-	-	-	-	-
501-550	2	2	-	-	-	-	-
951-1,000	1	-	-	-	-	-	-
1,001-1,050	1	-	-	-	-	-	-
1,101-1,150	1	-	-	-	-	-	-
1,201-1,250	1	-	-	-	-	-	-
Total fishermen	105	126	121	68	57	33	20

local fishermen quickly move to another lake where netting is more productive. However, according to Washburn (see footnote 2, p. 7), Birch Lake was reported to be one of the best cisco producing waters in the county, so apparently a few fishermen persisted and continued to intensively net the lake even when the population was low.

Catch per hour per net data given in Table 4 show conclusively that there was a marked reduction in the cisco spawning runs. The 1939 catch per hour data are only approximations, since total hours were not available because sets could be made from sunset to sunrise and could be pulled and reset. The 1943 catch per hour is probably low because it is based on research netting in which sets were made in various experimental ways, with all sizes of mesh nets, at all times of day, and at all depths. The 1944 through 1950 figures reflect fishing with the most productive size mesh on the most productive grounds during the most productive time. So the latter 7 years show best the population decline. The fishery was so poor by 1950 that census records were discontinued permanently, even though the population has since made somewhat of a comeback.

Table 4.--Catch data for the gill-net fishery in Birch Lake, 1939-1950

Year	Number of sets	Hours fished	Number of ciscoes	Ciscoes per hour per net
1939	766	4,596[a]	20,750	4.5 [a]
1943	87	638.6	2,108	3.07[b]
1944	582	2,888	18,137	6.28
1945	743	3,593	11,361	3.15
1946	651	3,356	3,600	1.07
1947	263	1,309	1,015	0.78
1948	280	1,740	417	0.24
1949	172	929	178	0.19
1950	43	215	37	0.17

[a] Based on 6 hours per set, the lawful set time beginning in 1944.

[b] Not comparable, since it is based on experimental netting.

COLLECTION OF DATA

Except for the netting records for 1939 and 1943-1950, the bulk of the data used in this study is obtained from scale samples taken by employees of the Michigan Department of Conservation and Mr. Gerald Breece of Williamsville, Michigan. Each scale envelope contains space for data on species, locality, date of collection, length, weight, sex, state of sex organs, gear used and name of collector. Depending on the year and the collector, the amount of data taken and its degree of accuracy varies considerably. Of course, the species of fish and the locality are present on all envelopes, as is the length measurement. Total length, the distance from the tip of the snout to the end of the compressed tail lobes, is used in this study. The date and weight measurement are present on all but a very few scale envelopes. In most cases there are enough fish in a sample so that these omissions are of minor importance. Unfortunately, extensive data on the state of the sex organs was collected only during the years 1946-1950. All ciscoes taken during the spawning season were caught in gill nets, but no records were kept on the size mesh of the nets, thus not allowing a thorough study of gill-net selectivity for the Birch Lake cisco.

Table 5 shows the variation in accuracy of the length and weight measurements taken during this time. For the purposes of this study total lengths are given to the nearest tenth of an inch and weight to the nearest tenth of an ounce. Since most of the fish were weighed only

Table 5.--Variation in precision in measurement of length and weight of Birch Lake ciscoes, 1937-1965

Year	Length: Nearest mm	Length: Nearest 0.1 in.	Length: Nearest 0.25 in.	Length: Nearest 0.5 in.	Weight: Nearest gram	Weight: Nearest ounce
1937	X	-	-	-	-	-
1939	X	-	-	-	X	-
1941	X	-	-	-	-	X
1943	X	-	-	-	-	X
1944	X	-	-	-	-	X
1945	X	-	-	-	-	X
1946	X	-	-	-	X	X
1947	-	X	-	-	-	X
1948	-	X	-	-	-	X
1949	-	X	-	-	-	X
1950	-	X	-	-	-	X
1952	-	-	X	-	-	X
1953	-	-	-	X	-	X
1954	-	X	-	-	-	X
1955	-	X	X	-	-	X
1956	-	X	-	X	-	X
1957	-	X	X	-	-	X
1958	-	X	X	-	-	X
1959	-	X	-	-	-	X
1960	-	X	-	-	-	X
1961	-	X	-	-	-	X
1962	-	-	X	-	X	X
1965	-	X	-	-	X	-

to the nearest ounce, this means using a higher degree of accuracy than that of the original data. However, it is felt this is necessary to make meaningful comparisons on tables. Statistical analyses are made on individual measurements to avoid introducing this inconsistency into the computations.

EXAMINATION OF SCALES

Scale samples from the cisco and other soft-rayed fishes are typically taken from the left side of the body in the area above the lateral line and below the origin of the dorsal fin. Unfortunately, ciscoes have quite deciduous scales and when the fish are gilled large numbers of scales are often lost. This is especially true in the smaller fish, which are not actually gilled or caught with the mesh behind the opercles as they try to retreat, but rather force themselves through the net until they are finally trapped with the mesh tight around the body, often near its mid-region. This removes many or all of the scales between the head and the entangled body area; thus, the desired scales are often absent. Therefore, the scale samples used in this study are not all from the same area of the body, a problem which will be discussed in a later section.

The scales were prepared for examination in three ways. Permanent mounts of whole scales were made on glass slides in a glycerin-gelatin mixture during the years 1939-1945. In 1944 impressions of some of the scales were made on cellulose acetate after softening of the plastic with acetone. Beginning in 1946 plastic impressions were made of scales from all of the fish sampled. In recent years these impressions were made with the use of a roller press such as that described by Smith (1954). It has been shown that this method does not distort the scale proportions and is quite simple to use, since no heat or softeners are required (Smith, 1954). The original scale samples are large enough so that plastic impressions could be made of scales from all fish for all years and these were used in studying the scales whenever possible. However, it was found that the whole mounts were sometimes easier to use. These were secondarily utilized with difficult-to-age scales from 1944 and 1945. The scales were studied with the aid of a microprojection machine such as that described by Moffett (1952), using a magnification of 44.3.

Van Oosten (1929) positively established the validity of the scale method for determining the age of this species in Lake Huron. Authors working with inland populations of ciscoes have also recognized the formation of a single age mark or annulus on the scale during the winter months when growth stops or slows down considerably (Carlander, 1945; Cooper, 1937; Fry, 1937; Hile, 1936). Since the fish in this study were captured in late autumn before the beginning of a new calendar year, the age of the fish can be determined simply by counting the number of annuli. However, since the fry hatch in the spring, it should be remembered that these fish have actually completed one more growing season than their age indicates. For example, a fish of age group III has lived through four growing seasons.

A problem arises when accessory annuli or checks are formed due to a temporary reduction in growth. Often one or more of these are present in a single year's growth field, and many of these checks are almost as distinct as the true annuli. There seems to be two theories as to when and why these checks are laid down on cisco scales. Fry (1937) found checks to be formed by only age-groups 0, I, II, and III because just the younger, fast-growing fish resume growth in the fall after the formation of the false summer annulus. The older, slow-growing fish do not resume growth, so the summer slowdown actually becomes a part of the true annulus. Hile (1936) found accessory annuli to occur regularly in the I, II, and III age-group fish in Muskellunge Lake, Wisconsin. Since very few older fish were collected, it is not known whether they also form checks in their later years. Van Oosten (1929) found accessory annuli to be most common during years with large growth increments, when the scales show more clearly the summer growth retardation. In the cisco this is usually the first 2 years of life, although rapid growth may also occur in older fish under very favorable conditions, as will be discussed later in this thesis. However, Smith (1956) found checks to be present in the scales of nearly all fish after the second year of life. This indicates that growth resumes in the fall in all age groups of this population, but that the older fish are more intolerant of unfavorable summer limnological conditions. Thus, they show a marked reduction in growth during this period while the younger age groups do not. Obviously, a combination of the above two factors in a population can result in the presence of, or absence of, false annuli in all the yearly growth fields on a given scale.

The formation of accessory annuli on the scales of Birch Lake ciscoes does not appear to follow any pattern, but varies greatly with the year. Fish captured during the slow-growth years of 1943-1945 commonly show checks in the first 2 years of growth. However, beginning with the third year it is difficult to determine if accessory annuli are present due to the very slow growth. When the growth rate began to increase quite rapidly in 1946 the fish started to form obvious checks in the later years, in addition to the earlier ones. This pattern agrees with that described by Fry (1937) and Van Oosten (1929). There are exceptions, however. Some scales fail to show any false annuli. This is especially obvious during the tremendous growth period following 1947 when the wide growth fields clearly lack checks. Throughout all the years it is very uncommon to find accessory annuli in the later years growth when none were formed during the first two growing seasons. The formation of checks varies with the year, the age of the fish during that year, the growth rate of the fish, and even with individuals of the same age group which are growing at approximately the same rate. Even as conditions in a lake vary there is a differential exposure of similar fish to these conditions. This necessitated several age determinations, in some cases as many as four, of most of the scales before a high degree of confidence in aging the scales was attained. Once the pattern of variability in the formation of checks was understood, however, the scales were reasonably easy to age.

LENGTH AND AGE AT CAPTURE

Comparison of sexes and totals

Table 6 gives the average length at each age of male and female ciscoes collected in 1939-1965. A one-way variance analysis at the 95% confidence level was run on the paired sex data for each age group for each year. Of the 49 comparisons of male and female lengths only 2, the II age group in 1946 and the I age group in 1959, show a significant variance between the sexes. In both instances the females were larger than the males. It is believed that a few such samples are expected in view of the total amount of data, and it is concluded that there is no significant difference in the lengths of male and female fish at the time of capture. Hile (1936) found there was a significant difference in the growth rates of males and females in Clear Lake, Wisconsin, but not in the other three lakes he studied, while Van Oosten (1929), Carlander (1945), Cooper (1937), Stone (1938), and Smith (1956) have found no such difference. The length measurements used throughout the rest of this study will be for the sexes combined.

Table 7 is a summary of the combined length and age data. The years 1943-1962 are most comparable since they are all represented by collections made during the same short fall spawning period. The 1937-1941 and 1965 collections were made during the summer, so the lengths would be expected to be somewhat smaller in comparison. Confidence limits were determined for the mean length for each age group for each

Table 6.--Comparison of length at capture of male and female ciscoes, 1939-1965

[Number of fish in parentheses]

Year	Age group and length in inches							
	I		II		III		IV	
	Male	Female	Male	Female	Male	Female	Male	Female
1939	-	8.3(1)	11.0(5)	11.3(1)	11.2(2)	11.1(1)	-	-
1943	-	12.6(1)	11.8(3)	12.0(1)	12.1(114)	12.0(33)	12.1(23)	12.1(5)
1944	-	-	12.0(13)	11.8(20)	12.2(109)	12.2(76)	12.4(23)	12.5(31)
1945	-	-	12.2(6)	12.3(35)	12.5(86)	12.6(427)	12.8(11)	12.8(103)
1946	-	-	12.1(3)[a]	12.9(7)	12.9(21)	13.1(569)	13.7(4)	13.2(58)
1947	-	-	13.3(1)	13.4(13)	13.5(23)	13.6(391)	14.1(4)	14.0(37)
1948	-	-	-	12.7(1)	13.6(1)	14.0(30)	14.2(2)	14.2(68)
1949	-	-	-	-	-	15.0(11)	16.3(2)	15.8(132)
1950	-	-	-	14.9(1)	-	-	15.2(3)	16.2(5)
1952	-	-	-	-	-	-	-	15.1(1)
1953	-	-	-	-	15.5(1)	15.2(3)	16.3(2)	16.6(8)
1954	-	-	14.6(1)	-	-	-	17.0(7)	17.2(7)
1955	11.8(24)	12.0(1)	11.5(1)	-	-	-	17.3(5)	17.4(3)
1956	11.5(10)	12.5(12)	-	-	-	-	-	17.1(2)
1957	-	-	13.9(24)	14.3(12)	-	15.7(1)	-	17.0(1)
1958	11.1(4)	-	13.5(1)	-	16.6(10)	17.0(23)	-	17.5(2)
1959	11.1(7)[a]	11.7(6)	-	-	17.1(5)	17.2(13)	-	-
1960	12.7(22)	12.9(1)	-	-	-	16.3(1)	-	-
1961	-	-	15.1(9)	15.0(18)	17.0(1)	-	-	17.8(2)
1962	10.5(37)	10.7(4)	15.4(4)	15.1(16)	-	-	-	18.8(2)
1965	12.0(1)	12.7(5)	14.5(5)	14.8(11)	-	-	-	-

(continued next page)

Table 6.--concluded

Year	Age group and length in inches							
	V		VI		VII		X	
	Male	Female	Male	Female	Male	Female	Male	Female
1939	-	-	-	-	-	-	-	-
1943	12.1(5)	14.0(1)	-	14.6(1)	-	-	-	17.6(1)
1944	14.0(2)	13.5(1)	14.4(1)	14.5(1)	-	18.1(1)	-	-
1945	13.1(3)	13.2(6)	14.9(3)	15.6(1)	-	-	-	-
1946	14.3(2)	13.6(5)	16.0(1)	-	-	-	-	-
1947	14.3(3)	14.1(3)	-	14.5(2)	-	16.3(1)	-	-
1948	-	14.6(7)	-	16.2(1)	-	-	-	-
1949	-	16.3(9)	-	18.3(1)	-	-	-	-
1950	16.4(3)	16.7(21)	-	-	-	-	-	-
1952	-	-	-	18.0(1)	-	18.8(1)	-	-
1953	18.2(3)	17.5(8)	-	19.3(1)	-	-	-	-
1954	17.1(1)	17.5(1)	16.0(1)	18.0(2)	-	-	-	-
1955	17.9(2)	17.9(8)	-	-	-	-	-	-
1956	-	17.1(4)	-	-	-	-	-	-
1957	-	-	19.5(1)	18.5(1)	-	-	-	-
1958	-	18.3(1)	20.5(1)	-	-	-	-	-
1959	-	-	-	-	-	-	-	-
1960	-	-	-	-	-	-	-	-
1961	-	-	-	-	-	-	-	-
1962	-	-	-	-	-	-	-	-
1965	-	-	-	-	-	-	-	-

[a] Significant difference between sexes.

Table 7.--Average total lengths of age groups of ciscoes captured in Birch Lake, 1937-1965[a]

[Number of fish in parentheses]

Year	Age group and length in inches							
	I	II	III	IV	V	VI	VII	X
1937[b]	9.5 (4)	10.3 (11)	-	13.3 (3)	-	-	15.4 (1)	-
1938[b]	9.3 (1)	10.4 (14)	11.2 (1)	-	-	-	-	-
1939[b]	8.2 (2)	11.0 (6)	11.1 (3)	12.4 (1)	-	15.8 (1)	-	-
1941[b]	-	-	-	-	-	15.8 (1)	-	-
1943	12.6 (1)	11.9 (4)	12.1 (147)	12.1 (33)	12.4 (6)	14.6 (1)	-	17.6 (1)
1944	-	11.9 (33)	12.2 (185)	12.5 (59)	13.8 (3)	14.5 (2)	18.1 (1)	-
1945	-	12.3 (41)	12.5 (513)	12.8 (114)	13.1 (9)	15.1 (4)	-	-
1946	-	12.7 (10)	13.1 (390)	13.3 (62)	14.1 (9)	16.0 (1)	-	-
1947	-	13.4 (14)	13.6 (414)	14.0 (41)	14.2 (6)	14.5 (2)	16.3 (1)	-
1948	-	12.7 (1)	13.9 (32)	14.2 (71)	14.6 (7)	16.2 (1)	-	-
1949	-	-	15.0 (11)	15.8 (134)	16.3 (9)	18.3 (1)	-	-
1950	-	14.9 (1)	-	15.9 (8)	16.7 (24)	-	-	-
1952	-	-	-	15.0 (1)	-	18.0 (1)	18.8 (1)	-
1953	-	-	15.3 (4)	16.5 (11)	17.8 (11)	-	-	-
1954	-	14.6 (1)	-	17.0 (17)	18.2 (3)	17.6 (4)	-	-
1955	11.9 (29)	12.4 (2)	-	17.4 (8)	17.9 (11)	-	-	-
1956	12.1 (24)	-	-	17.1 (2)	17.1 (4)	-	-	-
1957	-	14.0 (36)	15.7 (1)	17.0 (1)	-	19.0 (2)	-	-

(continued next page)

Table 7.--concluded

Year	Age group and length in inches							
	I	II	III	IV	V	VI	VII	X
1958	11.1 (4)	13.5 (1)	16.8 (33)	17.5 (2)	18.3 (1)	20.5 (1)	-	-
1959	11.4 (13)	-	17.2 (19)	-	-	-	-	-
1960	12.7 (23)	-	16.3 (1)	-	-	-	-	-
1961	-	15.0 (28)	17.0 (1)	17.8 (2)	-	-	-	-
1962	10.5 (41)	15.2 (20)	-	18.8 (2)	-	-	-	-
1965[b]	12.6 (6)	14.7 (16)	-	-	-	-	-	-

[a] Samples with a confidence limit of less than 5% of the mean are underlined.

[b] Non-spawning population.

year. Those samples with a confidence limit of less than 5% of the mean are underlined in Table 7 and are assumed to be good samples of the total population. The bulk of the data and the most useful data were collected in 1943-1950, since following the collapse of the fishery no extensive netting records or scale samples were taken.

Gear selectivity

It is obvious from Table 7 that the length ranges of the gill-net samples are small, since age groups with as few as four individuals (age-groups II in 1943 and V in 1956) show low confidence limits. Also there is only a small difference in average length between the best represented age groups, II-V, in 1943-1950. The differences between the average lengths of the II and V age groups of 1943-1948 are 0.5, 1.9, 0.8, 1.4, 0.8, and 1.9 inches respectively. In the 1943-1945 samples this may partly be due to the slow growth of the ciscoes after their second year. It was noted above that more rapid growth began during 1946 for all age groups over I, and although the difference between the average lengths of age groups does increase, this is expected because of the larger size of the fish captured.

These narrow and overlapping length ranges of age groups are more reasonably attributed to gill-net size selectivity. It can be seen that during 1943-1947 most of the fish matured at age III, or at the end of their fourth growing season. This would also be expected to be true of the stable population before 1943. The nets used by the fishermen, therefore, would be of such a size mesh as to exploit the most numerous spawning group, the III age group. It appears from the small numbers of individuals in the II and IV age groups that few fish mature at age II and that there is a heavy mortality after the fourth year of life. Hile (1936), Smith (1956), Carlander (1945) and Van Oosten (1929) all found the youngest mature fish of significant number to be age I, while Clemens (1922), Stone (1938), Cooper (1937), Dryer and Beil (1964), and Pritchard (1931) found this group to be age II. Brown and Moffett (1942) found the youngest mature cisco to be of age four (age-group III ?). In every lake the age at which the majority of the fish matured was the next older one, except for Lake Ontario (Pritchard, 1931) and Swains Lake, Michigan (Brown and Moffett, 1942). Probably a greater percentage of fish mature at age II than is shown, but were not taken in the gill nets due to the small size of the fish. The gill nets capture just the larger members of the group, so the average length of the II age group is almost as large as that for the III age group.

There is little doubt that there is a considerable mortality of fish after their fourth year. The fishery is probably the most important factor since it definitely selects the III age class. Van Oosten (1929) also found that each year class dropped off rapidly in the years following the year of its predominance, in this case the fourth, and attributed this to the intense fishery for lake herring. He also cited the paucity of old individuals as a symptom of heavy fishing. Old fish are also scarce in catches of ciscoes from Birch Lake (Table 7), and this is partly due to fishing mortality at younger ages. However, it must be remembered that the gill nets are of too small mesh to take the best sample of older fish. The smaller members of the IV and older age groups are selected for, resulting in low average lengths for these fish, especially the IV and V age groups. The few very large and old individuals are taken by entanglement or entrapment in the nets rather than by actual gilling. Dryer and Beil (1964, p. 508) write: "The small difference in size among the age groups is surely a result of the highly selective gill nets, segregation by maturity, and of selective fishing mortality." The fish captured in this study are segregated by maturity since the netting was carried out in a spawning population. So these three factors are active in the present study also.

Age composition

The age composition of the fish captured is shown in Table 8. It can be seen that the average age of the fish remains virtually constant during the years of 1943-1947, although the size of the fish increased considerably during this period. The question arises as to how the fishermen continued to take such a similar age sample when gill nets are so selective as to the size of fish that can be taken. Washburn (see footnote 2, p. 7), using both straight and experimental gill nets, found that 2 1/2- and 3-inch mesh nets were the most productive for taking the size of ciscoes then present in Birch Lake. The 2 1/2- and 3-inch meshes took approximately 75% of the total catch in experimental nets

Table 8.--Age composition of ciscoes captured in Birch Lake, 1937-1965

Year	Number of ciscoes	Percentage of total collection in each age group								Average age[a]
		I	II	III	IV	V	VI	VII	X	
1937	19	21.1	57.8	-	15.8	-	5.3	-	-	3.58
1938	16	6.25	87.5	6.25	-	-	-	-	-	3.00
1939	13	15.4	46.2	23.1	7.7	-	7.7	-	-	3.46
1941	1	-	-	-	-	-	100.0	-	-	-
1943	193	0.5	2.1	76.2	17.1	3.1	0.5	-	0.5	4.25
1944	283	-	11.7	65.4	20.8	1.1	0.7	0.3	-	4.15
1945	681	-	6.0	75.4	16.7	1.3	0.6	-	-	4.15
1946	472	-	2.1	82.7	13.1	1.9	0.2	-	-	4.15
1947	478	-	2.9	86.6	8.6	1.3	0.4	0.2	-	4.10
1948	112	-	0.9	28.6	63.4	6.3	0.9	-	-	4.78
1949	153	-	-	7.2	86.3	5.9	0.7	-	-	5.00
1950	33	-	3.0	-	24.2	72.7	-	-	-	5.42
1952	3	-	-	-	33.3	-	33.3	33.3	-	6.67
1953	26	-	-	15.4	42.3	42.3	-	-	-	5.27
1954	26	-	3.8	-	69.3	11.5	15.4	-	-	5.35
1955	50	58.0	4.0	-	16.0	22.0	-	-	-	3.24
1956	30	80.0	-	-	6.7	13.3	-	-	-	2.73
1957	40	-	90.0	2.5	2.5	-	5.0	-	-	3.28
1958	42	9.5	2.4	78.5	4.8	2.4	2.4	-	-	3.95
1959	32	40.6	-	59.4	-	-	-	-	-	3.19
1960	25	92.0	-	4.0	-	-	-	4.0	-	2.32
1961	31	-	90.3	3.2	6.5	-	-	-	-	3.16
1962	63	65.1	31.7	-	3.2	-	-	-	-	2.35
1965	22	27.3	72.7	-	-	-	-	-	-	2.73
Total	2,844									

[a] Total age is one year greater than the age group.

having mesh sizes of 1 1/2, 2, 2 1/2, 3, and 4 inches. Local fishermen in the Cass County area confirm that this size mesh net was used when the cisco population was still high. In order to continue to take a sample with a similar age structure in 1947 when the fish were averaging almost 2 inches more in length, it is obvious that the size of mesh must have been increased by the local fishery. Serious cisco fishermen who net a number of lakes own several sizes of nets. This is necessary since the size of the cisco populations and the size of the fish themselves vary greatly within the cluster of lakes in Cass County. The fishermen start out the season in a given lake by experimenting with different mesh nets until the most productive size is found. Often a number of fishermen will combine their efforts and compare results so that this can be determined more rapidly. Even those fishermen who concentrate their effort on a single lake own a number of nets, knowing that the effectiveness of a given mesh size may vary from year to year. Because of this flexibility of the fishery, it is felt that the age and length data collected during 1943-1950 are comparable and that all 8 years' catches are equally good samples of the population.

The problem of the effect of gill-net selectivity on age composition is certainly a difficult one. Authors such as Hile (1936) and Van Oosten (1929), who have also used gill-net samples of ciscoes, have dealt with this problem extensively and should be consulted for a more thorough discussion of the problem. Hile (1936) emphasizes that the overlap of length distributions of consecutive age groups of the cisco makes length alone a poor index of age, with the largest fish frequently not being the oldest. It is felt that the necessity in the present study is to establish the validity of comparisons. Table 9 gives the length distribution by age group of the ciscoes taken during 1943-1950. It shows quite well the extensive overlap of length ranges due to gill-net selectivity, but at the same time a striking similarity in the distribution pattern for the various years. Even though the predominant age group shifted from III in 1943-1947 to IV in 1948 and 1949 and to V in 1950, the overlap of lengths is still obvious enough to show that certain age groups were reduced in the population, rather than selected against by the gill nets.

All data for 1952 through 1962 were obtained mainly through the efforts of Mr. Gerald Breece of Williamsville, Michigan, a successful gill-net fisherman on Birch Lake for a number of years. The data are a representative sample of his catch during the spawning season and are comparable and useful in growth and life-history studies where comparisons between years are made. Nothing can be construed about the size of the cisco population from the numbers of fish in each year's sample.

Relation between population size, age, size frequency, and length

Table 9 shows strikingly the rapid increase in the size of the ciscoes during 1943-1950. In 8 years the distribution moves from one centering closely about 12 inches to one stretching between 15 and 18 inches. This increase in size is due to a reduction in population as

Table 9.--Length distribution by age group for the cisco, 1943-1950

Total length (inches)	Year, age group, and number of fish															
	1943				1944				1945				1946			
	II	III	IV	V	II	III	IV	V	II	III	IV	V	II	III	IV	V
10.0-10.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10.5-10.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11.0-11.4	-	1	-	1	4	1	-	-	1	3	-	-	-	-	1	-
11.5-11.9	3	55	11	1	15	38	6	-	7	23	1	-	1	3	[illegible]	-
12.0-12.4	1	77	17	1	11	109	27	-	21	180	20	-	1	26	3	-
12.5-12.9	-	14	5	2	5	30	18	-	11	254	53	5	5	114	7	-
13.0-13.4	-	1	-	-	-	4	6	-	1	69	31	1	3	182	34	2
13.5-13.9	-	-	-	-	-	-	1	2	-	4	9	1	-	59	10	2
14.0-14.4	-	-	-	1	-	-	-	-	-	-	-	2	-	3	5	2
14.5-14.9	-	-	-	-	-	-	-	1	-	-	-	-	-	1	2	2
15.0-15.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15.5-15.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16.0-16.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
16.5-16.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17.0-17.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17.5-17.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18.0-18.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

(continued next page)

Table 9.--concluded

Total length (inches)	Year, age group, and number of fish															
	1947				1948				1949				1950			
	II	III	IV	V	II	III	IV	V	II	III	IV	V	II	III	IV	V
10.0-10.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10.5-10.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11.0-11.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11.5-11.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12.0-12.4	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12.5-12.9	2	14	-	-	1	-	1	-	-	-	-	-	-	-	-	-
13.0-13.4	7	141	5	-	-	8	3	-	-	-	-	-	-	-	-	-
13.5-13.9	3	187	16	1	-	4	20	1	-	-	-	-	-	-	1	-
14.0-14.4	2	64	10	5	-	15	26	1	-	3	4	-	-	-	-	-
14.5-14.9	-	3	9	-	-	4	16	4	-	3	7	-	1	-	1	-
15.0-15.4	-	-	-	-	-	1	5	-	-	1	27	-	-	-	-	1
15.5-15.9	-	2	-	-	-	-	-	1	-	2	43	3	-	-	-	1
16.0-16.4	-	-	-	-	-	-	-	-	-	1	35	2	-	-	5	8
16.5-16.9	-	-	-	-	-	-	-	-	-	-	15	2	-	-	-	6
17.0-17.4	-	-	-	-	-	-	-	-	-	-	3	2	-	-	-	4
17.5-17.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3
18.0-18.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

indicated in Figure 2, which plots catch per hour (as an estimate of population size) with the average length of the four best represented age groups for 1943-1950. The catch figure for 1943 is omitted because it is based on experimental netting. Figure 2 shows conclusively that as the number of fish in the population decreases the length of the individual fish increases. This is a common occurrence in fish populations where competition is keen and a reduction in numbers means better conditions for those remaining. Hile (1936) found in the four lakes he studied that the order of the rate of growth was the reverse of the order with respect to population density. He attributed this to competition for food, or a "space factor" such as crowding. The question of why the population declined will be discussed later.

Table 10 gives the length distribution of the cisco for the entire study. By using it and Tables 7 and 8 the overall history of the cisco population in Birch Lake can be reviewed. It is known the cisco population was high during the 1930's (personal communications with fishermen). Even though the collections were made during the summer, the small size of the fish captured in 1937-1939 emphasize this. The large number of fish in the very young age groups show these fish were collected experimentally and not during the spawning season. After the reopening of the lake the spawning population was still high, but on the decline. The age structure remained remarkably stable while population numbers decreased through 1947. This indicates an even suppression of all groups of the population. Then, in 1948, there

Figure 2.--Comparison of catch and length of ciscoes, 1943-1950.

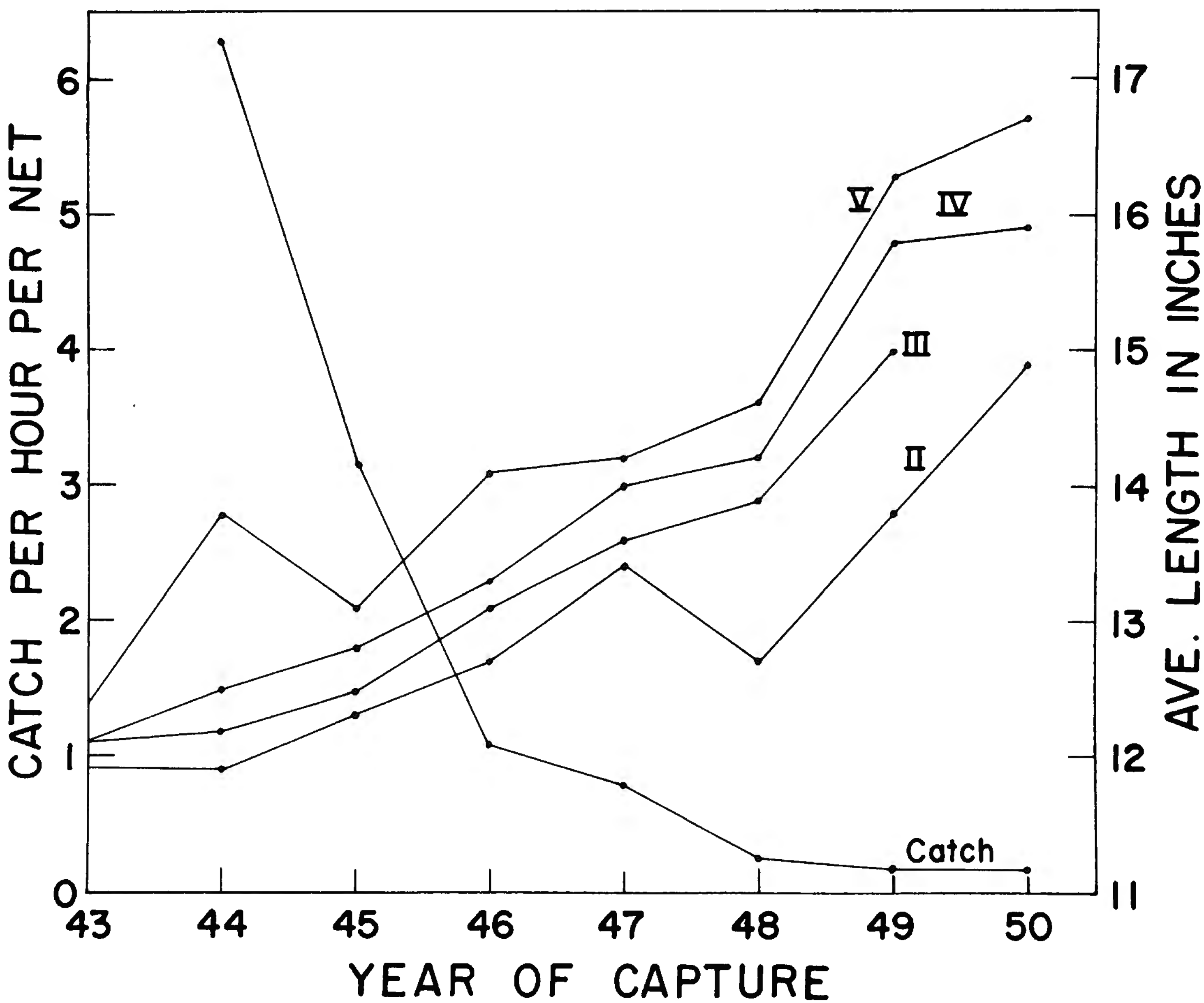

CATCH PER HOUR PER NET
AVE. LENGTH IN INCHES
YEAR OF CAPTURE
0
1
2
3
4
5
6
11
12
13
14
15
16
17
43
44
45
46
47
48
49
50
V
IV
III
II
Catch

Figure 2

Table 10.--Length distribution of the cisco, 1939-1965

Total length (inches)	Year and number of fish																				
	1939	1943	1944	1945	1946	1947	1948	1949	1950	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1965
8.5- 8.9	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9.0- 9.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9.5- 9.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10.0-10.4	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	16	-
10.5-10.9	4	-	1	-	-	-	-	-	-	-	-	-	2	3	-	2	1	-	-	33	-
11.0-11.4	5	2	4	-	-	-	-	-	-	-	-	-	3	1	-	-	7	-	-	2	-
11.5-11.9	-	70	59	-	-	-	-	-	-	-	-	-	7	1	-	1	4	-	-	-	-
12.0-12.4	-	96	147	221	30	1	-	-	-	-	-	-	13	-	-	1	-	4	-	-	3
12.5-12.9	-	21	51	303	126	16	2	-	-	-	-	-	5	7	2	-	1	12	-	-	4
13.0-13.4	-	1	10	102	221	153	11	-	-	-	-	-	1	5	4	-	-	7	-	-	3
13.5-13.9	-	-	3	14	71	207	25	-	1	-	-	-	-	4	10	1	-	-	-	-	-
14.0-14.4	-	1	2	2	10	84	42	7	-	-	-	-	-	-	12	-	-	-	4	1	-
14.5-14.9	-	1	2	1	5	13	24	10	2	-	-	1	1	-	5	-	-	-	6	2	4
15.0-15.4	-	-	-	2	-	2	2	27	1	1	2	1	-	-	1	-	-	-	13	11	4
15.5-15.9	-	-	-	1	-	2	2	48	1	-	2	-	-	-	3	2	-	-	4	4	2
16.0-16.4	-	-	-	-	2	1	-	38	13	-	3	5	3	1	-	5	1	1	1	2	1
16.5-16.9	-	-	-	-	-	-	-	17	6	-	5	4	-	1	-	13	1	-	-	-	1
17.0-17.4	-	-	-	-	-	-	-	5	4	-	4	5	4	1	1	4	10	-	1	-	-
17.5-17.9	-	1	-	-	-	-	-	-	4	-	5	3	3	2	-	9	7	-	1	1	-
18.0-18.4	-	-	1	-	-	-	-	1	1	1	2	5	5	1	1	3	-	-	1	-	-
18.5-18.9	-	-	-	-	-	-	-	-	-	1	2	-	3	-	1	-	-	-	-	-	-
19.0-19.4	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1	-	-	-
19.5-19.9	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	1	-
20.0-20.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-

was a definite lack of the usual recruitment into the younger age-groups III and II, corresponding to the 1945 and 1946 year classes respectively. The 1946 year class continued very poor in 1949, showing only 11 fish in the III age group, formerly by far the most dominant group. Nevertheless, there were significant numbers of the 1945 year class appearing in the IV age group, indicating the decline was probably greater in the 1946 than in the 1945 year class. More striking, however, was the complete absence of the 1947 year class as the II age group. In 1950 the population again had aged. The 1945 year class continued to predominate over 1946 with the result that the V age group was most numerous. A few fish of the poor 1946 year class were present in IV. The 1947 year class was again nonexistent as the III age group. There was only a single II recruit from the 1948 year class. It would appear that something happened starting in 1945 that resulted in very poor reproduction and year classes.

The population level was so low that no fish were netted in 1951, and in 1952 only 3 fish were taken. These fish belonged to the same year classes which were present in the 1950 sample. No fish ever appeared from the 1947 year class. Apparently the 1948, 1949, and 1950 year classes were somewhat improved since these fish began to show belatedly in 1953 as the V, IV, and III age groups. The same three year classes were again present in 1954, and a single recruit appeared from the 1952 year class. It is obvious that by 1954 reproduction was much improved, as shown by the large number of 2-year-old fish, or age-group I, that appeared in 1955 and 1956. Apparently the cisco will mature at a younger age if a normal spawning population of older fish does not exist. It is known that about this time the population made a comeback, although it peaked at a considerably lower level than before. The data seem to indicate that the population was still unstable since certain age groups are often completely missing in a year's sample. However, it is felt this is due partly to the fact that the sample was based on one man's netting, rather than to the existence of a "sick" population. Mr. Breece reports total catches of ciscoes for himself and an average of two other netters as 862 during the spawning season of 1960, 136 in 1961, 830 in 1962, 1,194 in 1963, and 329 in 1964. This indicates a considerable cisco population since these figures represent only a fraction of the total taken from Birch Lake. Mr. Breece feels a 10,000 estimate of ciscoes taken in 1963 would be conservative (personal communication). This estimate is fully one-half of the number taken during the high population of 1939 and 1943, and, considering the much greater size of the fish in recent years, Birch Lake appears to have regained much of its former production of ciscoes. It should be realized that nothing certain can be said about the size of the population after 1950; however, the available data do indicate the resumption of a more normal population structure.

To summarize, the average age figures in Table 8 can give a simple understanding of the changes in the cisco population. In 1943-1947 mostly age-group-III fish were taken, so the average age remained stationary around 4 years. Then the population began to grow older in 1948 with the onset of poor reproduction, and remained so until 1954. The year 1955 marked the return of younger fish to the spawning population. The fish were maturing so much younger that the fishery now also took large numbers of fish of ages I and II, depressing the average age even lower than it had been in the early 1940's. It seems reasonable to assume that the present fishery selects these more numerous younger mature fish, as it did the III age group previously.

GROWTH

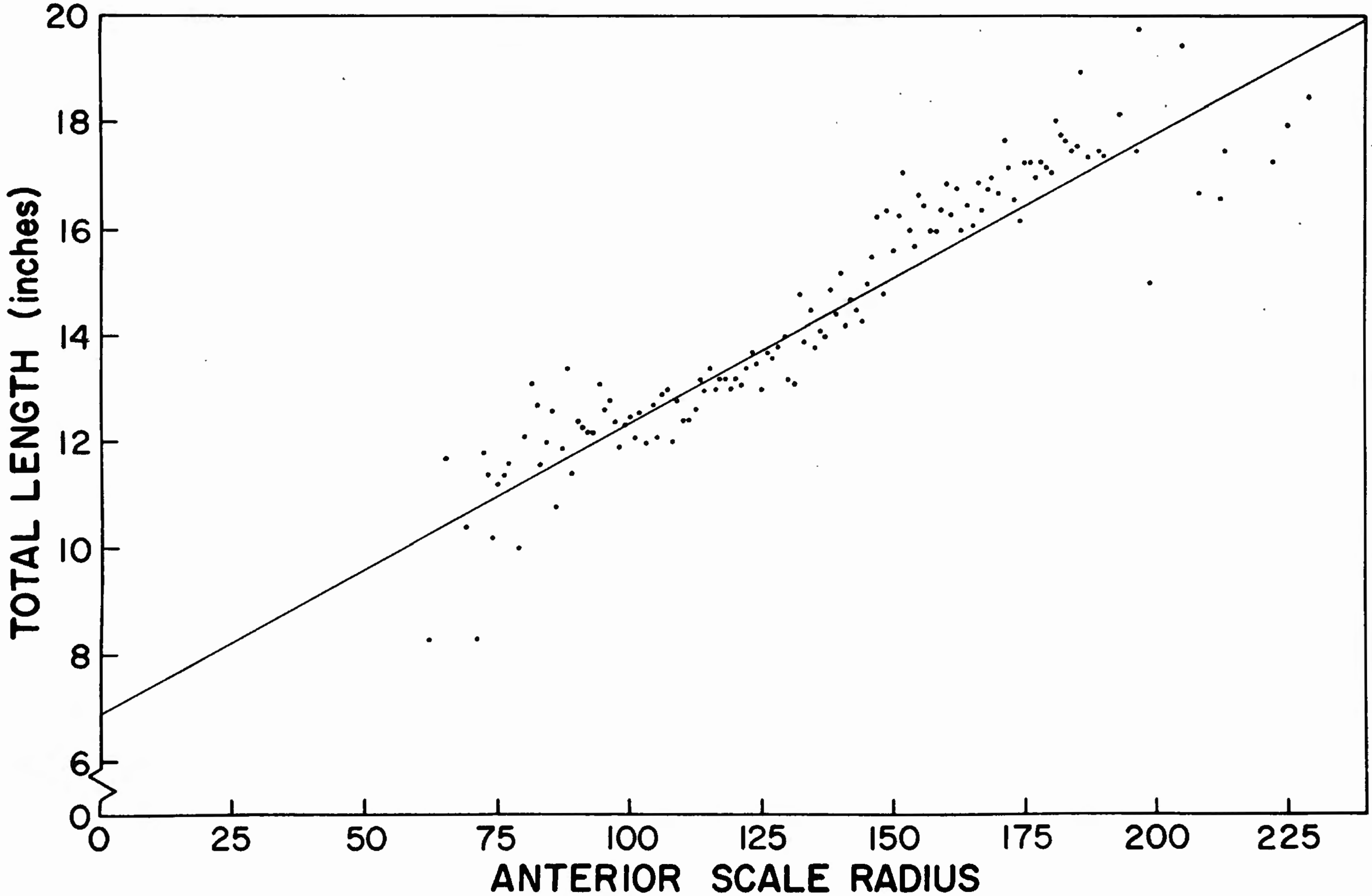
Body-scale relationship

In order to study the growth of fish from their scales it is necessary to establish a relationship between the growth of the body of the fish and the growth of the scale. For reasons which will be discussed later, it was necessary to use the anterior radius of the scale for the study of growth. This is the length of the scale between the center of the focus and the anterior edge of the scale. Using a magnification of 44.3, the total length of the radii of the scales of 1,226 fish were measured and plotted against the total length of the fish. Following the method suggested by Whitney and Carlander (1956), the mean body lengths at various scale measurements were determined and the unweighted data are shown on Figure 3. A regression of body length on scale measurement was run on the 1,226 fish and the regression line is drawn through the data. The linear regression equation is

$$L = 6.97352 + 0.054338\ S$$

where L is the total length of the fish in inches and S is the magnified scale radius in millimeters. It is obvious that this equation is erroneous, since it implies that the fish were almost 7 inches long when they formed their scales. Van Oosten (1929) found scale formation begins when the fish are only 35 to 40 millimeters long. It should be emphasized that there is little chance of error in measurement, since

Figure 3.--Relation between total length and magnified anterior scale radius (mm x 44.3) of the Birch Lake cisco.


TOTAL LENGTH (inches)
20
18
16
14
12
10
8
6
0
0
25
50
75
100
125
150
175
200
225
ANTERIOR SCALE RADIUS
Figure 3

it does not involve any age determination, but simply the measuring of the total length of the radius. Carlander (1945) states that the main objection to the use of radii measurements in growth calculations of coregonids is that the foci are large and it is often difficult to determine the center. However, he found this was not a problem in his material, and similarly it was not found to be a problem in this study since the foci are quite small.

Numerous factors could contribute to the erroneous body-scale ratio. Van Oosten (1929), who first established the validity of growth computations for the lake herring, found that scales of the same fish may grow at different relative rates, and that scales taken from the same area of the body grow more nearly at the same rate than those from various parts of the body. Thus it is desirable to use similar scales from each fish, preferably the very same scale or scales (key scales) in order to find the true relationship. However, as was discussed earlier, these criteria are not met in this study and the scale samples often are not taken even from the same general area of the body. It is obvious from examination of the scales that scale shape and size varies widely, even for fish of the same length. For smaller, younger fish the sample often tends to contain large, somewhat elongated scales, while the samples taken from larger, older fish often contain small, depressed scales. The reason for this bias is not known. Some workers average the lengths of several scales from the same fish to minimize this variability. This was not done in this study. Where possible, an attempt was made to use a scale with the same general shape for the growth measurements. Since there often would be only one of these present in the sample from a given fish, it was felt that averaging its measurement with the length of the radius from a differently shaped scale would only add more error.

Van Oosten (1929) also found that the various areas of a single scale may increase in length at different relative rates. He concluded that the diameter of a lake herring scale increases more in proportion to the increase in body length than does the anterior radius. He found that after formation of the first annulus the ratio of total scale diameter to total body length is so nearly constant that a direct-proportion relationship can be used in the back-calculation of growth. Most authors working on the age and growth of the cisco have recognized this and used diameter measurements and the direct-proportion calculation of growth (Hile, 1936; Cooper, 1937; Stone, 1938; Smith, 1956; Dryer and Beil, 1964). It was not possible to use diameter measurements in this study for several reasons. One, cited also by Carlander (1945), is that the annuli are very difficult to locate in the posterior field of the scale, especially in older, slow-growing fish and fish older than 3 years taken during the high-population, slow-growth years. Another, and perhaps the most important reason, is the fact that the posterior field of the scale is covered with skin. This skin has been allowed to dry on the scale for up to 20 years, and the plastic impressions made with these scales show a very indistinct posterior field. Van Oosten (1929) and Hile (1936) were able to scrub their scales clean in water before examination. However, this could not be satisfactorily done in this study. Cisco scales are quite thin and fragile and it was found that the amount of scrubbing needed to remove the dry skin ruins the structure of the scales and the water causes them to crinkle and bend. It was concluded that anterior radii measurements were the only ones that could be feasibly used.

Carlander (1945) is the only other investigator found to have used this particular measurement in his calculations. He discovered that the relationship between the scale radius and standard length is not a straight line but can be best described by a third degree parabola. A plot of the data given in his paper shows that his curve is very nearly a straight line, much more so than that shown in Figure 3. The correlation coefficient $r = \Sigma xy / \sqrt{\Sigma x^2 \cdot \Sigma y^2}$ for the data in the present study is 0.682 which is probably significant only because of the large sample involved (1,226 fish). It is very possible that the data could be better fitted to a curve other than a linear one. However, it was decided not to pursue this further since it is obvious that the lower end of the line bends up anyway, and any more exact curve would only cross the Y axis at a higher point, thus making the size at scale formation more ridiculous. Smith (1956), using diameter measurements, calculated a regression equation of

$$L = 0.01615 + 0.05486\ S$$

where L is total length in inches and S is the magnified scale diameter in millimeters. It is interesting to note that the slope of his line (0.05486) is very similar to the one found in this study (0.054338).

Smith, however, used direct-proportion calculations since his intercept was so small that it could be assumed to be zero. The materials and methods used in this study give a poor indication of the size of the ciscoes at scale formation.

Because of these problems it was decided to calculate growth with the use of the direct-proportion method, using the equation

$$\frac{\text{Length of scale radius in annulus of year X}}{\text{Total length of scale}} = \frac{\text{Total length of fish at end of year X}}{\text{Total length of fish at time of capture}}$$

where scale lengths are in millimeters and total lengths in inches. No exact comparisons may be made between the resultant data and that calculated by authors using more suitable material. Nevertheless, it is believed that important comparisons can be made between the growth shown by the ciscoes under various population densities within the same lake, if the same method is used throughout. Whitney and Carlander (1956) explain this very well in the following quote. Regression [1] refers to the regression of body length, L, on scale measurement, S, of the type, $L = a_1 + b_1 S$, run in this study. The Lea method is the use of direct proportion, or $L = b S$. They write (p. 21-22), ". . . Lea's method of back-calculation is not a regression method. It is, on the other hand, based upon an assumption that the growth of the body and scale are directly proportional. It is usually recognized that this method gives an approximation since the body-scale regression rarely, if ever, passes through the 0, 0 intercept. The use of this method assumes that the value of "a" in regression (1) is not great enough to significantly affect the computations. It would be of value in most cases to test this assumption. For general surveys and many management purposes growth approximations using the direct proportion computations are probably sufficiently accurate but it should always be recognized that they are approximations. Body-scale regressions differ for each species and probably for populations within species (Carlander, 1950a). Computation of regressions using small samples or even large samples with small size ranges might introduce more errors in the "corrected" growth computations than the errors resulting from the direct proportion assumption." The samples used in the present study had narrow size ranges because of the highly selective gill nets used to capture the fish. Most of the variation in scale length within the total sample occurs in this narrow range and this tends to level off the regression line horizontally, as shown by the very high intercept in Figure 3. Since Van Oosten (1929) and Smith (1956), using more precise materials, have proven that "a" is very small for other populations of Coregonus artedi, it is felt that the above assumption is applicable to the Birch Lake cisco and would be verified if more appropriate material were available.

Calculated growth

The method for computing average lengths was that suggested by Van Oosten (1953). Many authors investigating the age and growth of this species have recognized "Lee's phenomenon," or the decrease with age in the computed values of corresponding years of life (Van Oosten, 1929; Cooper, 1937; Hile, 1936; Smith, 1956; Fry, 1937; and Stone, 1938). Van Oosten (1929), Hile (1936), and Smith (1956) all found this phenomenon to occur among age groups of different year classes and also among different age groups of the same year class. Discrepancies among age groups of different year classes will be discussed first.

Table 11 gives the calculated length at the end of each year of every age group captured in the various years. Fifty fish per age group were selected at random to serve as the basis for calculation when a sample larger than that number was present in a given age group. Otherwise the total number of fish of each age was used. In this study, there is no general decrease with age in the calculated lengths at the end of the first year of life as expected. This is the growth year which caused so much difficulty in calculating the body-scale ratio, so it is not surprising that the use of the direct-proportion method apparently does not give good estimates for the first year's growth.

Lee's phenomenon is present almost without exception at the end of every year after the first during the years 1943-1950 for the

Table 11.--Growth of ciscoes captured in 1937-1965

Year	Age group	Number of fish	Average length at capture	Length at end of year of life in inches										
				1	2	3	4	5	6	7	8	9	10	11
1937[a]	II	4	9.5	4.1	9.0	9.5	-	-	-	-	-	-	-	-
	VII	1	15.4	4.0	9.7	11.5	12.4	13.3	14.4	15.0	15.4	-	-	-
1939[a]	I	2	8.3	4.9	8.3	-	-	-	-	-	-	-	-	-
	II	6	11.0	5.7	9.5	11.0	-	-	-	-	-	-	-	-
	III	3	11.1	5.5	9.4	10.4	11.1	-	-	-	-	-	-	-
1941[a]	VI	1	15.8	5.0	11.2	12.8	14.0	15.1	15.8	-	-	-	-	-
1943	I	1	12.6	7.0	12.6	-	-	-	-	-	-	-	-	-
	II	4	11.9	4.8	10.1	11.9	-	-	-	-	-	-	-	-
	III	50	12.1	4.8	10.1	11.4	12.1	-	-	-	-	-	-	-
	IV	33	12.1	5.1	9.7	10.9	11.6	12.1	-	-	-	-	-	-
	V	6	12.4	4.9	9.5	10.7	11.5	12.0	12.4	-	-	-	-	-
	VI	1	14.6	6.3	9.7	11.9	12.8	13.2	14.2	14.6	-	-	-	-
	X	1	17.6	4.6	8.8	10.5	11.7	12.7	13.7	14.8	15.6	16.4	17.2	17.6
1944	II	33	11.9	5.0	10.4	11.9	-	-	-	-	-	-	-	-
	III	50	12.2	5.0	10.1	11.5	12.2	-	-	-	-	-	-	-
	IV	50	12.5	5.1	9.9	11.0	11.8	12.5	-	-	-	-	-	-
	V	3	13.8	4.7	9.4	10.7	11.8	12.7	13.8	-	-	-	-	-
	VI	2	14.5	5.0	10.0	10.9	11.8	12.5	13.7	14.5	-	-	-	-
	VII	1	18.1	6.9	10.9	12.4	13.8	15.4	16.3	17.4	18.1	-	-	-
1945	II	41	12.3	5.3	11.3	12.3	-	-	-	-	-	-	-	-
	III	50	12.2	4.9	10.5	11.6	12.2	-	-	-	-	-	-	-
	IV	50	12.8	5.3	10.3	11.5	12.3	12.8	-	-	-	-	-	-
	V	9	13.1	5.0	9.5	10.8	11.7	12.5	13.1	-	-	-	-	-
	VI	4	15.1	4.5	10.0	12.0	13.2	14.0	14.6	15.1	-	-	-	-

(continued next page)

Table 11.--continued

Year	Age group	Number of fish	Average length at capture	Length at end of year of life in inches							
				1	2	3	4	5	6	7	8
1946	II	10	12.7	5.3	11.4	12.7	-	-	-	-	-
	III	50	13.1	5.4	10.8	12.3	13.1	-	-	-	-
	IV	50	13.3	5.3	10.1	11.3	12.4	13.3	-	-	-
	V	9	14.1	5.1	9.7	11.2	12.4	13.4	14.1	-	-
	VI	1	16.0	5.4	11.5	12.6	13.3	14.2	15.1	16.0	-
1947	II	14	13.4	5.0	11.6	13.4	-	-	-	-	-
	III	50	13.6	5.1	10.5	12.1	13.6	-	-	-	-
	IV	41	14.0	5.0	10.1	11.6	12.8	14.0	-	-	-
	V	6	14.2	5.1	10.0	11.3	12.3	13.3	14.2	-	-
	VI	2	14.5	4.8	10.3	11.7	12.5	13.4	14.0	14.5	-
	VII	1	16.3	3.8	8.1	9.2	10.3	11.8	13.3	15.1	16.3
1948	II	1	12.7	5.6	10.7	12.7	-	-	-	-	-
	III	32	13.9	5.2	10.6	12.3	13.9	-	-	-	-
	IV	50	14.2	4.9	9.8	11.5	12.9	14.2	-	-	-
	V	7	14.6	4.4	8.9	10.4	12.3	13.4	14.6	-	-
	VI	1	16.2	5.3	10.5	11.9	13.2	14.4	15.3	16.2	-
1949	III	11	15.0	4.7	10.7	12.7	15.0	-	-	-	-
	IV	50	15.8	4.9	10.0	11.7	13.5	15.8	-	-	-
	V	9	16.3	5.0	9.6	11.4	12.5	14.2	16.3	-	-
	VI	1	18.3	4.3	11.7	13.0	14.5	15.6	16.6	18.3	-
1950	II	1	14.9	4.5	9.7	14.9	-	-	-	-	-
	IV	8	15.9	4.7	10.4	12.6	14.9	15.9	-	-	-
	V	24	16.7	4.7	10.1	11.8	13.5	15.8	16.7	-	-
1952	IV	1	15.0	3.6	8.8	11.9	14.1	15.0	-	-	-
	VI	1	18.0	3.6	9.8	12.5	14.6	15.9	16.9	18.0	-
	VII	1	18.8	4.9	10.1	12.4	13.7	15.5	16.9	18.1	18.8

(continued next page)

Table 11.--continued

Year	Age group	Number of fish	Average length at capture	Length at end of year of life in inches-							
				1	2	3	4	5	6	7	8
1953	III	4	15.3	3.5	7.7	12.9	15.3	-	-	-	-
	IV	11	16.5	4.0	9.1	12.7	15.2	16.5	-	-	-
	V	11	17.8	4.5	10.5	13.8	15.9	17.0	17.8	-	-
1954	II	1	14.6	4.4	10.5	14.6	-	-	-	-	-
	IV	17	17.0	3.9	8.9	13.2	15.7	17.0	-	-	-
	V	3	18.2	4.6	10.2	14.0	16.1	16.9	18.2	-	-
	VI	4	17.6	4.1	9.9	13.0	15.1	16.3	17.1	17.6	-
1955	I	29	11.9	7.3	11.9	-	-	-	-	-	-
	II	2	12.4	3.8	8.9	12.4	-	-	-	-	-
	IV	8	17.4	4.3	9.0	13.3	15.9	17.4	-	-	-
	V	11	17.9	4.5	9.8	13.6	16.1	17.1	17.9	-	-
1956	I	24	12.1	6.8	12.1	-	-	-	-	-	-
	IV	2	17.1	4.0	9.9	12.8	15.1	17.1	-	-	-
	V	4	17.1	3.7	8.9	12.7	15.1	16.2	17.1	-	-
1957	II	36	14.0	6.1	10.3	14.0	-	-	-	-	-
	III	1	15.7	4.2	10.3	13.8	15.7	-	-	-	-
	IV	1	17.0	4.4	9.6	13.5	15.2	17.0	-	-	-
	VI	2	19.0	4.1	8.2	13.9	16.1	17.3	18.3	19.0	-
1958	I	4	11.1	5.4	11.1	-	-	-	-	-	-
	II	1	13.5	3.1	6.9	13.5	-	-	-	-	-
	III	33	16.8	6.0	10.4	14.3	16.8	-	-	-	-
	IV	2	17.5	3.6	8.9	13.1	16.3	17.5	-	-	-
	V	1	18.3	2.8	6.2	12.0	15.1	17.3	18.3	-	-
	VI	1	20.5	5.9	9.9	14.9	17.8	19.2	20.0	20.5	-

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Table 11.--concluded

Year	Age group	Number of fish	Average length at capture	Length at end of year of life in inches							
				1	2	3	4	5	6	7	8
1959	I	13	11.4	6.9	11.4	-	-	-	--	-	-
	III	19	17.2	6.0	10.8	14.2	17.2	-	-	-	-
1960	I	23	12.7	7.1	12.7	-	-	-	-	-	-
	III	1	16.3	4.9	9.4	13.7	16.3	-	-	-	-
	VII	1	19.0	3.8	10.2	13.1	15.2	16.2	17.2	18.1	19.0
1961	II	28	15.0	6.7	12.5	15.0	-	-	-	-	-
	III	1	17.0	6.6	10.4	14.9	17.0	-	-	-	-
	IV	2	17.8	5.1	9.9	13.9	16.9	17.8	-	-	-
1962	I	41	10.5	5.7	10.5	-	-	-	-	-	-
	II	20	15.2	6.7	12.4	15.2	-	-	-	-	-
	IV	2	18.8	5.7	10.6	14.5	17.6	18.8	-	-	-
1965[a]	I	6	12.6	5.7	12.6	-	-	-	-	-	-
	II	16	14.7	6.4	12.1	14.7	-	-	-	-	-

[a] Final year of growth not completed.

well represented age-groups II through V. The only three exceptions are the IV and V age groups at the end of the fifth year of life in 1944, the same situation in 1946, and the II and IV age groups at the end of the second year of life in 1950. Since there are only 3 fish in the V age group in 1944 and 1 fish in the II age group in 1950, the only significant exception is that in 1946. In all other instances during these years the average calculated lengths of age-groups II-V decrease or remain the same as the age increases. The consistency with which this phenomenon occurs indicates that the calculated lengths after the first year of life are fairly good ones.

Many of the authors who have recognized Lee's phenomenon among age groups of different year classes have given various explanations which Smith (1956) has summarized into four principal ones. They are:

1. Selective action of gill nets used in collecting fish
2. Segregation as to maturity during the spawning run
3. Segregation as to size, independent of maturity
4. Higher mortality rate among fast-growing fish than among slow-growing

All but the third one contribute to this phenomenon in the Birch Lake cisco. It has been shown how the gill-net fishery selects the larger, fast-growing fish in the younger age groups and the smaller, slow-growing fish in the older age groups. Therefore, the computed lengths for the earlier years of life are greater in the younger age groups. Van Oosten (1929) found that the faster-growing members of a given year class tend to mature at a younger age. Since this study is based on a spawning population, it is reasonable to assume that only the larger members of the II age group are sexually mature and present in the sample. Similarly, the ciscoes that mature later in life are the slow-growing ones in their year class. This undoubtedly is a major factor in the presence of Lee's phenomenon. The fishery causes a higher mortality among fast-growing fish since they can be taken at a younger age and are more exposed to the fishery. In addition, there is the possibility cited by Hile (1936) and Carlander (1945) that slow-growing individuals may be naturally longer-lived than fast-growing ones. Both factors would decrease the calculated lengths with increasing age, since fast-growing fish progressively disappear from the older age groups. The explanation due to segregation as to size, regardless of maturity, is not applicable to this study since only the spawning population is sampled.

Lee's phenomenon may also occur in comparisons of the growth of fish of the same year class captured at different ages. Table 12 gives the growth of ciscoes of year classes 1939-1946 and 1955. These year classes were selected because they had a good representation of fish captured at various ages. Again Lee's phenomenon is well pronounced after the first year of life in comparing age-groups II-V, although there are more exceptions than in Table 11. The regular occurrence of Lee's phenomenon in both comparisons (Tables 11 and 12) seems to support one assumption made in comparing age groups of different year classes

Table 12.--Growth of ciscoes of various year classes

Year class	Age group	Number of fish	Average length at capture	Length at end of year of life in inches: 1	2	3	4	5	6	7	8
1939	IV	33	12.1	5.1	9.7	10.9	11.6	12.1	-	-	-
	V	3	13.8	4.7	9.4	10.7	11.8	12.7	13.8	-	-
	VI	4	15.1	4.5	10.0	12.0	13.2	14.0	14.6	15.1	--
1940	III	50	12.1	4.8	10.1	11.4	12.1	-	-	-	-
	IV	50	12.5	5.1	9.9	11.0	11.8	12.5	-	-	-
	V	9	13.1	5.0	9.5	10.8	11.7	12.5	13.1	-	-
	VI	1	16.0	5.4	11.5	12.6	13.3	14.2	15.1	16.0	-
	VII	1	16.3	3.8	8.1	9.2	10.3	11.8	13.3	15.1	16.3
1941	II	4	11.9	4.8	10.1	11.9	-	-	-	-	-
	III	50	12.2	5.0	10.1	11.5	12.2	-	-	-	-
	IV	50	12.8	5.3	10.3	11.5	12.3	12.8	-	-	-
	V	9	14.1	5.1	9.7	11.2	12.4	13.4	14.1	-	-
	VI	2	14.5	4.8	10.3	11.7	12.5	13.4	14.0	14.5	-
1942	I	1	12.6	7.0	12.6	-	-	-	-	-	-
	II	33	11.9	5.0	10.4	11.9	-	-	-	-	-
	III	50	12.2	4.9	10.5	11.6	12.2	-	-	-	-
	IV	50	13.3	5.3	10.1	11.3	12.4	13.3	-	-	-
	V	6	14.2	5.1	10.0	11.3	12.3	13.3	14.2	-	-
	VI	1	16.2	5.3	10.5	11.9	13.2	14.4	15.3	16.2	-
1943	II	41	12.3	5.3	11.3	12.3	-	-	-	-	-
	III	50	13.1	5.4	10.8	12.3	13.1	-	-	-	-
	IV	41	14.0	5.0	10.1	11.6	12.8	14.0	-	-	-
	V	7	14.6	4.4	8.9	10.4	12.3	13.4	14.6	-	-
	VI	1	18.3	4.3	11.7	13.0	14.5	15.6	16.6	18.3	-

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Table 12.--concluded

Year class	Age group	Number of fish	Average length at capture	Length at end of year of life in inches							
				1	2	3	4	5	6	7	8
1944	II	10	12.7	5.3	11.4	12.7	-	-	-	-	-
	III	50	13.6	5.1	10.5	12.1	13.6	-	-	-	-
	IV	50	14.2	4.9	9.8	11.5	12.9	14.2	-	-	-
	V	9	16.3	5.0	9.6	11.4	12.5	14.2	16.3	-	-
1945	II	14	13.4	5.0	11.6	13.4	-	-	-	-	-
	III	32	13.9	5.2	10.6	12.3	13.9	-	-	-	-
	IV	50	15.8	4.9	10.0	11.7	13.5	15.8	-	-	-
	V	24	16.7	4.7	10.1	11.8	13.5	15.8	16.7	-	-
	VII	1	18.8	4.9	10.1	12.4	13.7	15.5	16.9	18.1	18.8
1946	II	1	12.7	5.6	10.7	12.7	-	-	-	-	-
	III	11	15.0	4.7	10.7	12.7	15.0	-	-	-	-
	IV	8	15.9	4.7	10.4	12.6	14.9	15.9	-	-	-
	VI	1	18.0	3.6	9.8	12.5	14.6	15.9	16.9	18.0	-
1955	I	24	12.1	6.8	12.1	-	-	-	-	-	-
	II	36	14.0	6.1	10.3	14.0	-	-	-	-	-
	III	33	16.8	6.0	10.4	14.3	16.8	-	-	-	-

(Table 11), namely, that growth does not vary with the calendar year. Better growth in certain calendar years could not cause Lee's phenomenon within age groups of the same year class, but could cause this discrepancy when comparing different year classes. For example, in the 1943 collection in Table 11, if the 1939 year class (age-group IV) grew more slowly during its second year of life than the 1940 year class (age-group III) did in its second year of life, then the difference in length at the end of the second year could be due to variations in growth during the second year of life of year classes which passed that year during different calendar years, and not to the factor cited above by Smith (1956). Since there was a progressive increase in the size of the ciscoes in Birch Lake, better growth in some calendar years undoubtedly contributes to the more regular appearance of Lee's phenomenon when comparing different year classes (Table 11). However, the presence of Lee's phenomenon in a comparison of age groups of the same year classes (Table 12) shows that three of the factors recognized by Smith (1956) are operative in both comparisons.

Comparison of growth of
year classes

Hile (1936) described what he called a "cisco-type" of growth which is typical of this species. It is characterized by rapid growth in length during the first or first and second years of life, with a gradual decrease in growth thereafter. Cooper (1937) emphasizes that the first prominent decrease in growth occurs in the year during which sexual maturity is first attained. A study of the length increments given in Table 13 confirms that this pattern of growth is shown by the Birch Lake ciscoes taken in 1937-1950. Under high population densities, growth is rapid during the first 2 years and declines quickly thereafter. During this time there is no significant increase in the first and second years' growth, but there is a slight increase in the calculated growth during the third and fourth years of life as the population declined in the late 1940's. This increased growth in the later years is responsible for the yearly increases in the size of fish of a given age. The population was very low by 1950 and it never fully recovered to previous levels. Concurrent with this population change was a marked change in the growth pattern of the cisco. In the years following 1950, the third year's growth continued to increase until, in many cases, it approaches or even exceeds that attained during the first or second year of life. The fourth year's growth is now two or three times greater than that for this growing season during the high population levels. Figure 4 compares the growth curves of three year classes. These year classes were chosen because a reasonably large sample of fish was present from each in a number of successive years. The 1942 year class is represented by 140 fish in five age groups, the 1950 year class by 32 fish in three age groups, and the 1955 year class by 93 fish in three age groups. The growth histories of these fish are combined to get the respective growth curves, which are representative of that shown under various population

Table 13.--Growth increments of ciscoes computed from Table 11, 1937-1965

Year	Age group	Length increment in inches during year of life										
		1	2	3	4	5	6	7	8	9	10	11
1937[a]	II	4.1	4.9	0.5	-	-	-	-	-	-	-	-
	VII	4.0	5.7	1.8	0.9	0.9	1.1	0.6	0.4	-	-	-
1939[a]	I	4.9	3.4	-	-	-	-	-	-	-	-	-
	II	5.7	3.8	1.5	-	-	-	-	-	-	-	-
	III	5.5	3.9	1.0	0.7	-	-	-	-	-	-	-
1941[a]	VI	5.0	6.2	1.6	1.2	1.1	0.7	-	-	-	-	-
1943	I	7.0	5.6	-	-	-	-	-	-	-	-	-
	II	4.8	5.3	1.8	-	-	-	-	-	-	-	-
	III	4.8	5.3	1,3	0.7	-	-	-	-	-	-	-
	IV	5.1	4.6	1.2	0.7	0.5	-	-	-	-	-	-
	V	4.9	4.6	1.2	0.8	0.5	0.4	-	-	-	-	-
	VI	6.3	3.4	2.2	0.9	0.4	1.0	0.4	-	-	-	-
	X	4.6	4.2	1.7	1.2	1.0	1.0	1.1	0.8	0.8	0.6	0.4
1944	II	5.0	5.4	1.5	-	-	-	-	-	-	-	-
	III	5.0	5.1	1.4	0.7	-	-	-	-	-	-	-
	IV	5.1	4.8	1.1	0.8	0.7	-	-	-	-	-	-
	V	4.7	4.7	1.3	1.1	0.9	1.1	-	-	-	-	-
	VI	5.0	5.0	0.9	0.9	0.7	1.2	0.8	-	-	-	-
	VII	6.9	4.0	1.5	1.4	1.6	0.9	1.1	0.7	-	-	-
1945	II	5.3	6.0	1.0	-	-	-	-	-	-	-	-
	III	4.9	5.6	1.1	0.6	-	-	-	-	-	-	-
	IV	5.3	5.0	1.2	0.8	0.5	-	-	-	-	-	-
	V	5.0	4.5	1.3	0.9	0.8	0.6	-	-	-	-	-
	VI	4.5	5.5	2.0	1.2	0.8	0.6	0.5	-	-	-	-
1946	II	5.3	6.1	1.3	-	-	-	-	-	-	-	-
	III	5.4	5.4	1.5	0.8	-	-	-	-	-	-	-
	IV	5.3	4.8	1.2	1.1	0.9	-	-	-	-	-	-
	V	5.1	4.6	1.5	1.2	1.0	0.7	-	-	-	-	-
	VI	5.4	6.1	1.1	0.7	0.9	0.9	0.9	-	-	-	-
1947	II	5.0	6.6	1.8	-	-	-	-	-	-	-	-
	III	5.1	5.4	1.6	1.5	-	-	-	-	-	-	-
	IV	5.0	5.1	1.5	1.2	1.2	-	-	-	-	-	-
	V	5.1	4.9	1.3	1.0	1.0	0.9	-	-	-	-	-
	VI	4.8	4.5	1.4	0.8	0.9	0.6	0.5	-	-	-	-
	VII	3.8	4.3	1.1	1.1	1.5	1.5	1.8	1.2	-	-	-

(continued next page)

Table 13.--continued

Year	Age group	Length increment in inches during year of life										
		1	2	3	4	5	6	7	8	9	10	11
1948	II	5.6	5.1	2.0	-	-	-	-	-	-	-	-
	III	5.2	5.4	1.7	1.6	-	-	-	-	-	-	-
	IV	4.9	4.9	1.7	1.4	1.3	-	-	-	-	-	-
	V	4.4	4.5	1.5	1.9	0.9	1.2	-	-	-	-	-
	VI	5.3	5.2	1.4	1.3	1.2	0.9	0.9	-	-	-	-
1949	III	4.7	6.0	2.0	2.3	-	-	-	-	-	-	-
	IV	4.9	5.1	1.7	1.8	2.3	-	-	-	-	-	-
	V	5.0	4.6	1.8	1.1	1.7	2.1	-	-	-	-	-
	VI	4.3	7.4	1.3	1.5	1.1	1.0	1.7	-	-	-	-
1950	II	4.5	5.2	5.2	-	-	-	-	-	-	-	-
	IV	4.7	5.7	2.2	2.3	1.0	-	-	-	-	-	-
	V	4.7	5.4	1.7	1.7	2.3	0.9	-	-	-	-	-
1952	IV	3.6	5.2	3.1	2.2	0.9	-	-	-	-	-	-
	VI	3.6	6.2	2.7	2.1	1.3	1.0	1.1	-	-	-	-
	VII	4.9	5.2	2.3	1.3	1.8	1.4	1.2	0.7	-	-	-
1953	III	3.5	4.2	3.2	2.4	-	-	-	-	-	-	-
	IV	4.0	5.1	3.6	2.5	1.3	-	-	-	-	-	-
	V	4.5	6.0	3.3	2.1	1.1	0.8	-	-	-	-	-
1954	II	4.4	6.1	4.1	-	-	-	-	-	-	-	-
	IV	3.9	5.0	4.3	2.5	1.3	-	-	-	-	-	-
	V	4.6	5.6	3.8	2.1	0.8	1.3	-	-	-	-	-
	VI	4.1	5.8	3.1	2.1	1.2	0.8	0.5	-	-	-	-
1955	I	7.3	4.6	-	-	-	-	-	-	-	-	-
	II	3.8	5.1	3.5	-	-	-	-	-	-	-	-
	IV	4.3	4.7	4.3	2.6	1.5	-	-	-	-	-	-
	V	4.5	5.3	4.0	2.3	1.0	0.8	-	-	-	-	-
1956	I	6.8	5.3	-	-	-	-	-	-	-	-	-
	IV	4.0	5.9	2.9	2.3	2.0	-	-	-	-	-	-
	V	3.7	5.2	3.8	2.4	1.1	0.9	-	-	-	-	-
1957	II	6.1	4.2	3.7	-	-	-	-	-	-	-	-
	III	4.2	6.1	3.5	1.9	-	-	-	-	-	-	-
	IV	4.4	5.2	3.9	1.7	1.8	-	-	-	-	-	-
	VI	4.1	4.1	5.7	2.2	1.2	1.0	0.7	-	-	-	-
1958	I	5.4	5.7	-	-	-	-	-	-	-	-	-
	II	3.1	3.8	6.6	-	-	-	-	-	-	-	-
	III	6.0	4.4	3.9	2.5	-	-	-	-	-	-	-

(continued next page)

Table 13.--concluded

Year	Age group	Length increment in inches during year of life							
		1	2	3	4	5	6	7	8
1958	IV	3.6	5.3	4.2	3.2	1.2	-	-	-
(cont)	V	2.8	3.4	5.8	3.1	2.2	1.0	-	-
	VI	5.9	4.0	5.0	2.9	1.4	0.8	0.5	-
1959	I	6.9	4.5	-	-	-	-	-	-
	III	6.0	4.8	3.4	3.0	-	-	-	-
1960	I	7.1	5.6	-	-	-	-	-	-
	III	4.9	4.5	4.3	2.6	-	-	-	-
	VII	3.8	6.4	2.9	2.1	1.0	1.0	0.9	0.9
1961	II	6.7	5.8	2.5	-	-	-	-	-
	III	6.6	3.8	4.5	2.1	-	-	-	-
	IV	5.1	4.4	4.0	3.0	0.8	-	-	-
1962	I	5.7	4.8	-	-	-	-	-	-
	II	6.7	5.7	2.8	-	-	-	-	-
	IV	5.7	4.9	3.9	3.1	1.2	-	-	-
1965[a]	I	5.7	6.9	-	-	-	-	-	-
	II	6.4	5.7	3.6	-	-	-	-	-

[a] Final year of growth not completed.

Figure 4.--Growth of three year classes of ciscoes in Birch Lake.

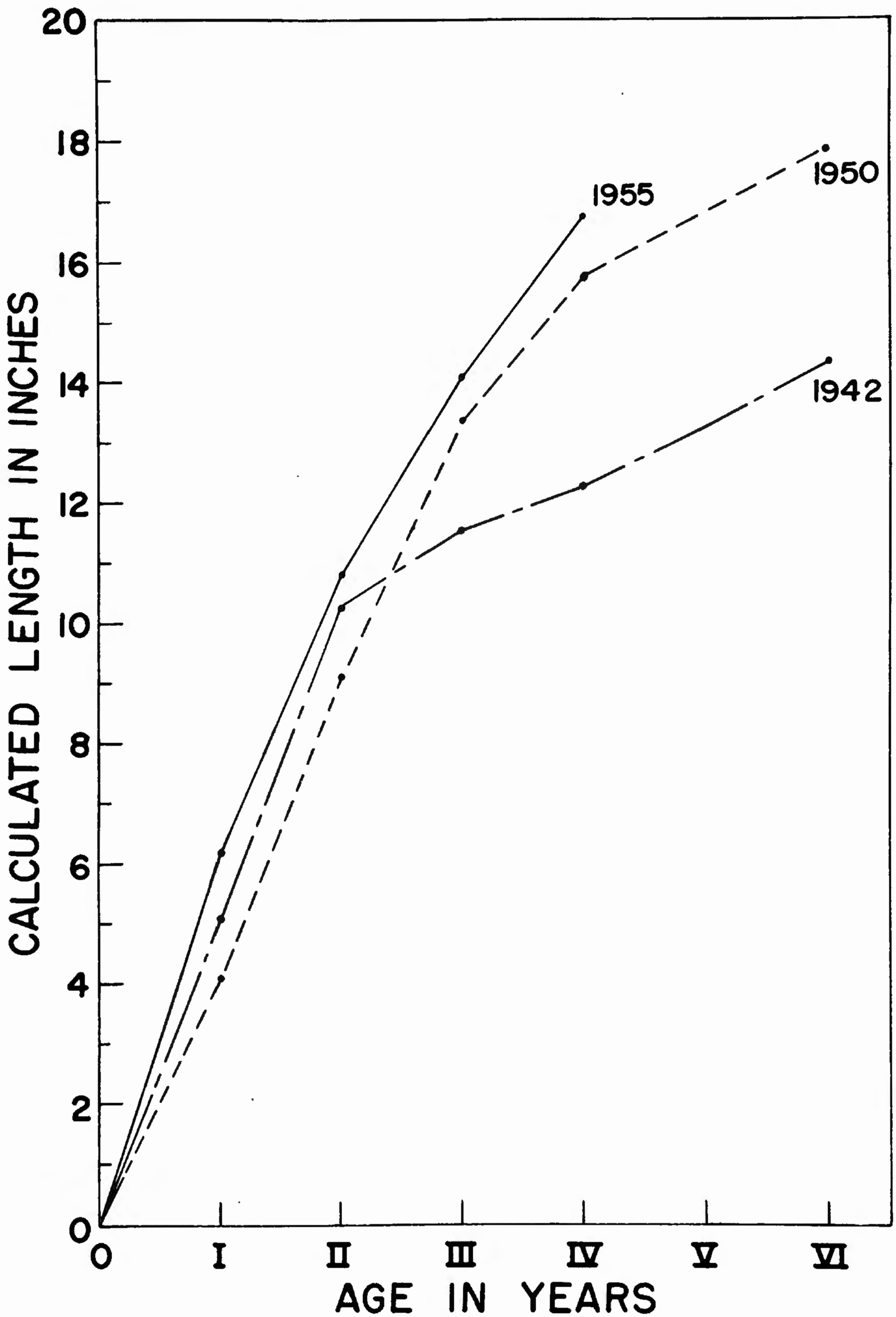

20
18
16
14
12
10
8
6
4
2
0
CALCULATED LENGTH IN INCHES
1955
1950
1942
O
I
II
III
IV
V
VI
AGE IN YEARS

Figure 4

densities. The marked decline in growth after the second year is easily seen in the 1942 curve. The 1950 curve does not begin to level off until the fourth year, and then it is not nearly as drastic as the 1942 curve. Even after 4 years the 1955 year class shows no marked decline in growth.

The growth curves are strikingly similar through the second year of life and only after this age do the curves diverge to any degree. It can be concluded that ciscoes during their first 2 years do not compete with the rest of the population of ciscoes, since their growth is independent of the overall population density. Birch Lake apparently can provide suitable conditions for these young ciscoes, regardless of their numbers, within the limits of the species. This conclusion of density independence of growth during the first 2 years is made with the assumption that the numbers of fish captured in older age groups is indicative of the numerical strength of a year class at all ages. The argument that young fish were equally abundant throughout the study but died before they were captured during the so-called low-density periods does not seem justified. During the third year of life these fish enter into competition with the rest of the population and, under high density, this competition is severe and growth is greatly curtailed. Low population levels reduce this competition in the later years and favorable conditions for growth exist for these older fish as well as the young. Thus, the increase in length of various age groups of fish is not due to greater growth in the earlier years, but to a lengthening of the rapid growth period. Also, overall growth is not greatly limited by sexual maturity, as was expressed by Cooper (1937), since the fish captured during low population levels are mature yet continue to grow rapidly while forming the sex products.

WEIGHT AT CAPTURE

Comparison of sexes

Table 14 gives a comparison of the average weights at capture of male and female ciscoes of each age group. Since these fish are sexually mature it is expected that females of a given length or age will weigh more than males due to the greater weight of female sex products. A one-way variance analysis at the 95% confidence level shows that females weigh significantly more in 18 of the comparisons. The average weight of the males exceeds that of the females in only 5 of the 47 pairs of data, and these are not statistically significant. It is concluded that females weigh more than males of the same length. To prove this variation, one length-weight relationship was determined for 16 males captured in 1946 and one for 289 females captured the same year, the only year when length and weight were measured in millimeters and grams. The equations are:

Males $\log W = -4.66355 + 2.84880 \log L$ (corr. coef. = 0.66046)

Females $\log W = -2.27275 + 1.91409 \log L$ (corr. coef. = 0.59101)

where W is weight in grams and L is length in millimeters. The disparity between the two equations is illustrated in Figure 5.

Table 14.--Comparison of weight at capture of male and female ciscoes, 1939-1965[a]

[Number of fish in parentheses]

Year	Age group and weight in ounces							
	I		II		III		IV	
	Male	Female	Male	Female	Male	Female	Male	Female
1939[d]	-	2.5(1)	6.2(5)	6.7(1)	6.6(2)	6.4(1)	-	-
1943	-	11.0(1)	7.3(3)	8.0(1)	7.6(114)	8.5(33)	8.1(28)	9.4(5)
1944	-	-	8.0(2)	9.8(8)	8.8(29)	9.7(27)	9.3(9)	10.8(13)
1945	-	-	8.0(6)	10.0(35)	8.9(86)	10.6(427)	9.5(11)	10.8(103)
1946	-	-	9.4(3)[b]	11.6(7)	11.0(21)	12.6(369)	12.9(4)[c]	13.1(58)
1947	-	-	12.0(1)	13.6(13)	13.5(23)	14.0(391)	15.3(4)	14.9(37)
1948	-	-	-	9.0(1)	14.0(1)	15.0(30)	17.0(2)	17.0(68)
1949	-	-	-	-	-	27.7(11)	30.0(2)	30.3(132)
1950	-	-	-	26.0(1)	-	-	23.7(3)	30.4(5)
1952	-	-	-	-	-	-	-	28.0(1)
1953	-	-	-	-	22.0(1)	23.3(3)	27.5(2)	36.1(8)
1954	-	-	-	-	-	-	27.7(3)	35.5(4)
1955	10.3(10)	14.0(1)	10.0(1)	-	-	-	35.5(4)	32.5(2)
1956	8.7(10)	11.7(12)	-	-	-	40.0(1)	-	30.0(1)
1957	-	-	16.5(13)	19.4(7)	-	-	-	37.0(1)
1958	7.5(4)	-	14.0(1)	-	30.6(10)	37.2(23)	-	43.0(2)
1959	7.3(7)[b]	9.0(6)	-	-	30.0(5)	32.7(13)	-	-
1960	10.9(22)	12.0(1)	-	-	-	23.0(1)	-	-
1961	-	-	20.8(9)	22.4(18)	30.0(1)	-	-	-
1962	5.8(37)	6.1(4)	20.5(4)	22.1(16)	-	-	-	-
1965[d]	9.2(1)	10.3(5)	16.5(5)	15.9(11)	-	-	-	-

(continued next page)

Table 14.--concluded

Year	Age group and weight in ounces							
	V		VI		VII		X	
	Male	Female	Male	Female	Male	Female	Male	Female
1939[d]	-	-	-	-	-	-	-	-
1943	8.0(5)	12.0(1)	-	17.0(1)	-	-	-	31.0(1)
1944	14.0(1)	-	16.0(1)	18.0(1)	-	-	-	-
1945	10.0(3)	11.8(5)	15.8(3)	14.0(1)	-	-	-	-
1946	14.6(2)	14.6(5)	25.0(1)	-	-	-	-	-
1947	15.0(3)	16.0(3)	-	15.2(2)	-	19.0(1)	-	-
1948	-	17.4(7)	-	16.2(1)	-	-	-	-
1949	-	30.7(9)	-	-	-	-	-	-
1950	28.0(3)	34.1(21)	-	-	-	-	-	-
1952	-	-	-	41.0(1)	-	49.0(1)	-	-
1953	41.3(3)	42.8(8)	-	-	-	-	-	-
1954	-	39.0(1)	32.0(1)	32.0(1)	-	-	-	-
1955	36.0(2)	36.2(16)	-	-	-	-	-	-
1956	-	29.3(3)	-	-	-	-	-	-
1957	-	-	45.0(1)	48.0(1)	-	-	-	-
1958	-	48.0(1)	42.0(1)	-	-	-	-	-

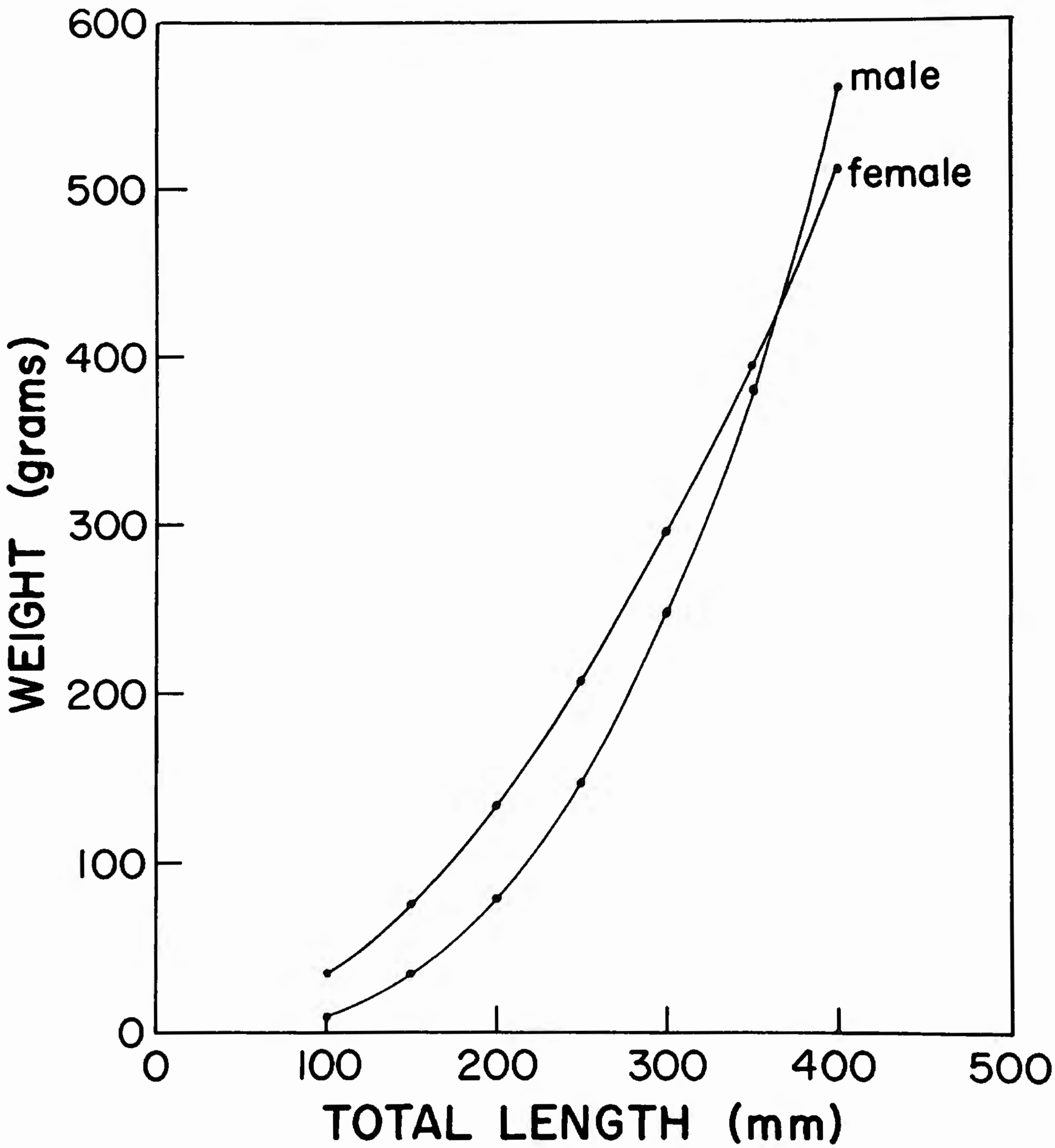
[a] Age groups underlined -- females significantly heavier than males.

[b] Females significantly longer than males.

[c] Males significantly longer than females.

[d] Non-spawning fish.

Figure 5.--Length-weight relations of male and female ciscoes captured in 1946.



male
female
WEIGHT (grams)
600
500
400
300
200
100
0
0
100
200
300
400
500
TOTAL LENGTH (mm)

Figure 5

Length-weight relationship and its variations

The cisco is known to show seasonal changes in weight of each sex correlated with the development of sex products (Smith, 1956). There are also definite variations in weight with the progress of the spawning season itself resulting from the release of eggs and sperm. A study of the females captured in 1946 verifies this. The state of the sex organs of 267 females is known, and Table 15 gives the average lengths and weights of the fish according to the progress of spawning. Although there is no significant difference in the average length, there is a definite difference in the average weight of ripe, partially spent, and spent fish (all statistically significant at the 95% level). An average loss of 17.1% (65.6 grams/382.7 grams) of the body weight is found between ripe and spent fish. Table 15 also shows the lengths and weights of five females before and after stripping. The loss in body weight of the five stripped fish is 18.8%, compared to the above figure of 17.1% for average loss, indicating very few eggs are reabsorbed after natural spawning. It also shows that the field methods used in determining the state of the gonads are reliable.

The relationship between length and weight would also be expected to vary with the year of capture, considering the length of the study and the changes in population densities and size of the fish. To test this, a length-weight relationship of the form $\log W = a + b \log L$ was determined for each year and the respective values of "a" and "b" are

Table 15.--Comparison of female weights at various stages of spawning, 1946

Fish as collected			
State of sex organs	Number of fish	Average length (mm)	Average weight (grams)
Spent	34	334.7	317.1
Partially spent	147	331.6	359.3
Ripe	86	332.4	382.7

5 females before and after artificial stripping			
Length (mm)	Weight before stripping	Weight after stripping	Percentage loss
341	438	358	18.3
333	362	303	16.3
334	395	320	19.0
336	409	338	17.4
342	411	318	22.6

shown in Table 16. W is expressed in ounces and L in inches. It is obvious that there is considerable yearly variation in this relationship. Part of this variation may be due to fluctuations in the sex composition of the sample, with a, the intercept, tending to be smaller (relatively) and b, the slope larger, when males are more numerous, and just the opposite when females are numerous. However, there is great variation in the 1946, 1947, 1948, 1949, and 1950 equations; yet all are composed largely of females.

Because of variations in the length-weight relationship with sex, season, year of capture, and progress of spawning, it was decided not to try to calculate growth in weight for this population. Since growth in weight would have to be based on the weight during spawning it is felt that this would not be indicative of the overall growth pattern. The following length-weight equation, expressing weight in ounces and length in inches, is based on all 2,567 fish for which length and weight measurements are available, regardless of sex, progress of spawning, age, or year of capture. It is meant to be only an indication of a so-called "average" situation, and certainly is applicable only to a spawning population. The equation is:

$$\text{Log } W = -3.18615 + 3.82606 \text{ Log } L$$

and is indicated in Figure 6. This and all the above length-weight equations were determined with the use of computers at the Computer Center of the University of Michigan. The length and weight measurements

Table 16.--Yearly variations in the values of a and b in the length-weight equation Log W = a + b log L

Year	Number of fish	a	b	Partial correlation coefficient	Percentage females
1939	11	-2.54048	3.20239	.98715	30.0
1943	198	-2.34403	3.00164	.76320	22.3
1944	111	-1.85196	2.58385	.73443	45.9
1945	680	-1.29568	2.09789	.52568	84.0
1946	478	-1.32276	2.16616	.59212	93.4
1947	478	-1.13757	2.01240	.58622	93.5
1948	112	-2.89824	3.56610	.78132	97.3
1949	153	-0.51959	1.66700	.60230	98.7
1950	33	-1.17752	2.19868	.63214	81.8
1953	26	-2.39880	3.21452	.83528	76.9
1954	11	-2.33524	3.14981	.88179	50.0
1955	29	-2.08460	2.90153	.95764	27.3
1956	27	-2.26283	3.02214	.97731	64.3
1957	24	-2.06159	2.91417	.96566	37.5
1958	42	-2.82333	3.55327	.96972	61.9
1959	32	-2.63093	3.34635	.99385	61.5
1960	25	-2.03078	2.77707	.98250	12.0
1961	31	-1.02408	2.01351	.83216	66.7
1962	62	-2.78837	3.47689	.99076	34.9
Total	2,567	-3.18615	3.82606	.93837	

Figure 6.--Total length-weight relation of ciscoes in Birch Lake.

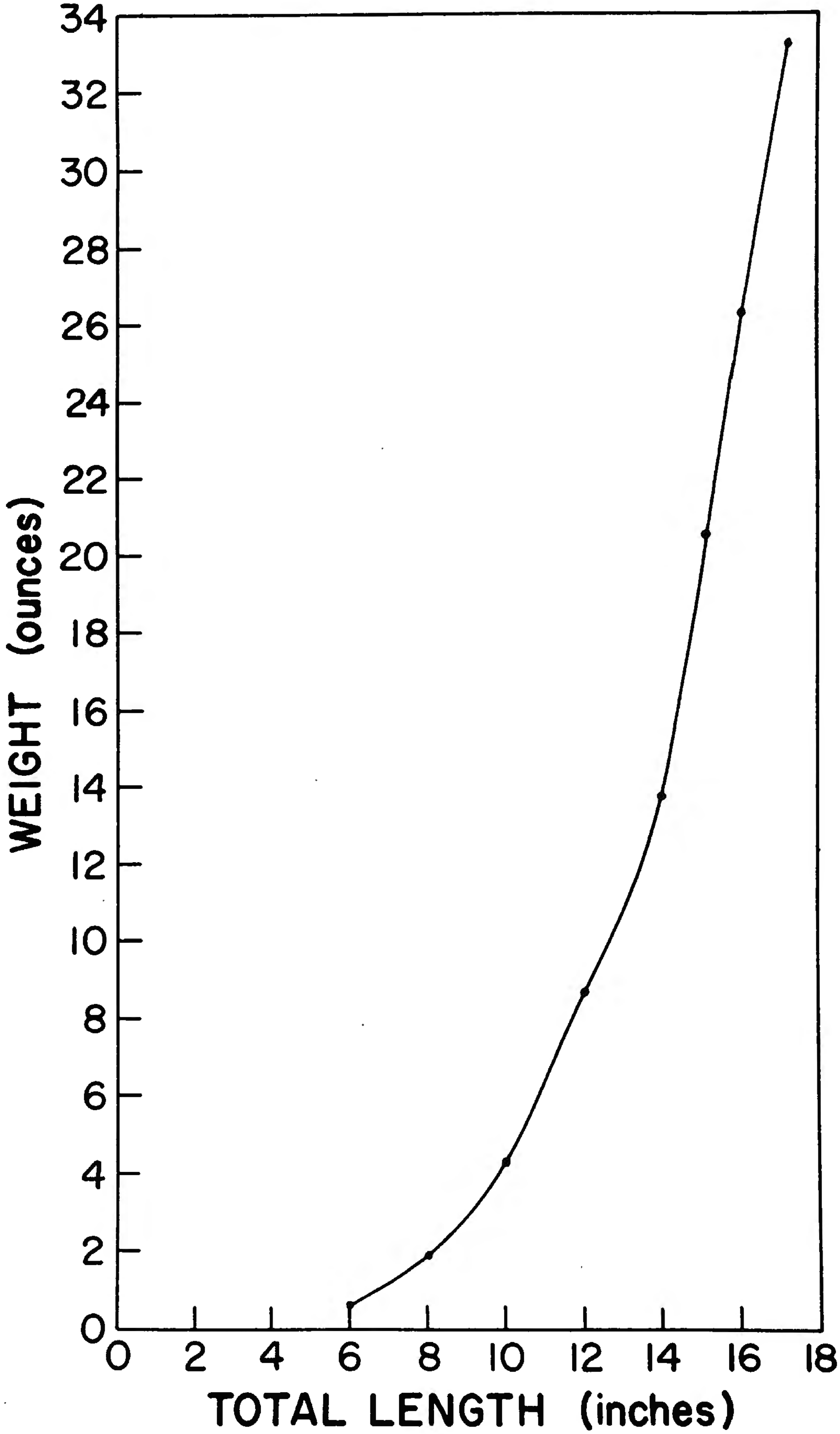

34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
WEIGHT (ounces)
0
2
4
6
8
10
12
14
16
18
TOTAL LENGTH (inches)

Figure 6

were converted to logarithms, entered on IBM cards, and fed into the computer, which then calculated the relationship between the two variables.

The partial correlation coefficients given in Table 16 for the various years are all highly significant at the 99% level, meaning the data fitted a log-log relationship well. The lowest correlation coefficients occurred during 1945-1950 when the samples were the largest. This is the period during which the growth pattern of the fish changed markedly in their later years. It may be that this change in growth pattern during the lives of these fish caused the length-weight relationship to deviate more from a log-log equation. Under more stable growth and population conditions the data fit this relationship better.

These lower correlation coefficients in 1945-50 are also undoubtedly partly a function of the fact that males taken during the spawning season more nearly fit a log-log length-weight relation than females. The correlation coefficient for 16 males taken in 1946 is .86046 while that for 289 females is only .59101. Since the fish captured in these years were mostly females (Table 16) this undoubtedly lowered the correlation. Length-weight relationships for each sex for each year were not determined since no calculation of growth in weight was undertaken.

SPAWNING

The spawning run of the cisco has been described in Birch Lake by Bowditch (1939) and Washburn (1944) (see footnotes 1 and 2, p. 7) and in various other bodies of water (Smith, 1956; Van Oosten, 1929; Stone, 1938; Scott, 1951; Dryer and Beil, 1964; Pritchard, 1931). All except Scott and Stone record that the abundance of the sexes varies throughout the run, with the males tending to arrive on the spawning grounds earlier than the females. The proportion of females then increases throughout the duration of the run. Stone (1938) did not find that the males preceded the females to any degree, but did discover that the males were fewer than the females later in the run. Table 17 gives the percentage of females captured in each day's collection made during the years 1943-1962. The totals for all years indicate that the males tend to be more numerous early in the season, although this trend can not be shown for many individual years because of the paucity of males. Totals for only 7 days (November 16, 17, 18, 21, 22, 25, and 26) contain a percentage of females of 60.5% or less, and these are all within the first 11 days of the season. To test further, the season was divided into two parts according to months and the percentage of the total fish of each sex taken during November was calculated. The results are shown in Table 18 and are somewhat inconclusive, since the percentage of males captured in the earlier month is greater than the percentage of females

Table 17.--Daily sex ratios of spawning ciscoes, 1943-1962

Year	Date and percentage of females														
	November														
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1943	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1944	-	-	-	-	-	-	-	-	-	33.3	51.8	-	-	86.7	0.0
1945	-	-	-	-	-	-	-	-	-	41.5	69.4	57.4	98.0	100.0	94.0
1946	-	-	-	-	-	-	-	80.0	-	-	66.7	-	-	-	-
1947	-	-	100.0	100.0	-	-	-	58.8	75.0	-	-	69.2	84.6	95.8	94.1
1948	-	100.0	-	-	-	-	83.3	-	94.1	96.0	100.0	100.0	100.0	-	-
1949	-	-	-	100.0	100.0	-	-	100.0	-	-	-	100.0	95.8	100.0	100.0
1950	-	-	-	-	75.0	-	-	100.0	-	-	-	-	-	-	100.0
1952	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1953	-	-	-	0.0	-	-	66.7	-	-	-	100.0	100.0	66.7	100.0	100.0
1954	-	33.3	42.9	100.0	-	-	100.0	-	-	-	60.0	50.0	-	-	-
1955	-	-	-	25.0	100.0	100.0	0.0	50.0	-	50.0	57.1	10.0	-	-	-
1956	-	-	-	-	-	-	-	-	-	-	-	66.7	100.0	-	-
1957	-	60.0	30.0	-	-	-	29.4	-	-	-	-	-	-	-	-
1958	-	66.7	100.0	100.0	66.7	-	-	-	-	-	-	-	57.1	50.0	-
1959	50.0	47.6	-	-	100.0	66.7	-	-	-	100.0	-	-	-	-	-
1960	-	-	-	-	-	-	-	-	-	-	-	-	-	12.0	-
1961	57.1	-	-	87.5	-	50.0	-	-	-	-	-	-	-	-	100.0
1962	100.0	50.0	-	-	-	-	-	-	-	100.0	-	-	-	-	-
Total percent females	57.9	53.3	52.2	72.4	82.4	60.0	43.3	74.1	86.2	60.5	58.6	67.1	91.4	83.1	94.2
Number of fish	19	45	23	29	17	10	30	54	29	76	244	117	151	154	103

(continued next page)

Table 17.--continued

Year	Date and percentage of females													
	December													
	1	2	3	4	5	6	7	8	9	10	11	14	15	17
1943	35.6	7.8	-	-	-	-	-	-	-	21.7	-	-	-	-
1944	-	-	-	23.1	28.1	100.0	32.3	41.7	0.0	0.0	-	-	-	-
1945	89.9	98.6	94.4	96.7	69.6	71.0	91.7	57.1	90.5	75.0	-	-	-	93.3
1946	-	95.1	90.0	93.7	100.0	96.0	88.0	90.9	100.0	100.0	100.0	62.5	-	-
1947	90.0	98.6	100.0	94.4	90.9	100.0	97.1	100.0	95.6	96.4	100.0	-	-	-
1948	-	100.0	100.0	100.0	-	100.0	-	-	-	-	-	-	-	-
1949	-	100.0	100.0	100.0	-	-	100.0	100.0	100.0	100.0	-	-	-	-
1950	-	87.5	100.0	-	-	-	-	-	62.5	-	-	-	-	-
1952	-	-	-	-	-	-	-	-	-	-	-	-	100.0	-
1953	-	-	100.0	0.0	-	100.0	-	100.0	-	-	-	-	-	-
1954	-	-	-	100.0	0.0	-	-	-	-	-	-	-	-	-
1955	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1956	75.0	-	-	50.0	100.0	-	60.0	-	-	-	-	-	-	-
1957	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1958	20.0	0.0	-	0.0	100.0	-	-	-	-	-	-	-	-	-
1959	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1960	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1961	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1962	38.7	-	-	-	-	-	20.0	-	-	-	-	-	-	-
Total percent females	66.1	80.5	94.4	86.1	71.1	89.7	66.9	73.2	92.7	75.0	100.0	62.5	100.0	93.3
Number of fish	168	277	162	180	114	97	139	71	109	100	25	8	3	30

(continued next page)

Table 17.--concluded

Year	Date and percentage of females					
	December					
	19	21	22	23	28	31
1943	-	-	-	-	-	-
1944	-	-	-	-	-	-
1945	-	-	-	-	-	-
1946	100.0	93.8	-	-	-	100.0
1947	-	-	-	-	-	-
1948	-	-	100.0	100.0	100.0	-
1949	-	-	-	-	-	-
1950	-	-	-	-	-	-
1952	-	-	-	-	-	-
1953	-	-	-	-	-	-
1954	-	-	-	-	-	-
1955	-	-	-	-	-	-
1956	-	-	-	-	-	-
1957	-	-	-	-	-	-
1958	-	-	-	-	-	-
1959	-	-	-	-	-	-
1960	-	-	-	-	-	-
1961	-	-	-	-	-	-
1962	-	-	-	-	-	-
Total percent females	100.0	93.8	100.0	100.0	100.0	100.0
Number of fish	12	16	2	3	9	53

Table 18.--Percentage of total catch of each sex of ciscoes taken during November

Year	Percentage of total females	Percentage of total males
1944	78.6	58.2
1945	40.0	56.9
1946	7.0	29.0
1947	24.8	67.7
1948	71.0	100.0
1949	67.1	100.0
1950	38.5	33.3
1953	65.0	83.3
1954	90.9	87.5
1956	16.7	10.0
1958	92.3	56.3
1962	23.5	94.3

in only 7 of the 12 years where collections were made during both months. It appears that the time differential in the arrival of the sexes on the spawning grounds is not always pronounced in Birch Lake, but varies with the year.

Smith (1956) found that in his spawning collections the percentage of spent male lake herring is always greater than of females. This was also noted in Birch Lake by Bowditch (see footnote 1, p. 7). The collections made in the present study for which extensive data were taken on the state of the sex organs (years 1946 and 1947) contain so few males that no significant comparisons can be made. Smith (1956) also found that older fish spawn earlier than young fish, and that longer fish spawn first. Table 19 gives the percentage of fish in each age group for each day's collection in Birch Lake from 1943 to 1950. No trend toward earlier spawning of older fish can be determined, with the proportions in each age class remaining roughly the same throughout the season. A one-way variance analysis run on 86 ripe and 181 spent or partially spent females captured in 1946 shows no significant difference at the 95% level in their lengths (see Table 15). Therefore, neither of Smith's observations is supported by the present study.

Table 19.--Percentage of total collection of ciscoes in each age group by date, 1943-1950

[Number of fish in parentheses]

Date		1943				1944			
		II-	III	IV	V+	II-	III	IV	V+
Nov.	25	-	-	-	-	16.7(1)	66.7(4)	16.7(1)	-
	26	-	-	-	-	10.6(18)	70.6(120)	18.8(32)	-
	29	-	-	-	-	13.3(2)	53.3(8)	33.3(5)	-
	30	-	-	-	-	-	100.0(1)	-	-
Dec.	1	4.4(2)	66.7(30)	24.4(11)	4.4(2)	-	-	-	-
	2	3.9(2)	80.4(41)	13.7(7)	2.0(1)	-	-	-	-
	4	-	-	-	-	-	84.6(11)	7.7(1)	7.7(1)
	5	-	-	-	-	25.0(8)	46.9(15)	21.9(7)	6.2(2)
	6	-	-	-	-	-	-	-	100.0(1)
	7	-	-	-	-	3.2(1)	64.5(20)	32.3(10)	-
	8	-	-	-	-	25.0(3)	50.0(6)	16.7(2)	8.3(1)
	9	-	-	-	-	-	-	-	100.0(1)
	10	-	82.6(19)	4.3(1)	13.0(3)	-	50.0(1)	50.0(1)	-

(continued next page)

Table 19.--continued

Date	1945				1946			
	II	III	IV	V+	II	III	IV	V+
Nov. 23	-	-	-	-	-	80.0(24)	16.7(5)	3.3(1)
25	4.9(2)	78.0(32)	12.2(5)	4.9(2)	-	-	-	-
26	-	83.3(30)	13.9(5)	2.8(1)	-	100.0(9)	-	-
27	11.1(6)	75.9(41)	13.0(7)	-	-	-	-	-
28	-	78.0(39)	20.0(10)	2.0(1)	-	-	-	-
29	1.7(1)	81.7(49)	16.7(10)	-	-	-	-	-
30	2.0(1)	74.0(37)	20.0(10)	4.0(2)	-	-	-	-
Dec. 1	6.3(5)	79.7(63)	12.7(10)	1.3(1)	-	-	-	-
2	2.7(2)	76.7(56)	19.2(14)	1.4(1)	4.9(2)	80.5(33)	12.2(5)	2.4(1)
3	14.8(8)	66.7(36)	16.7(9)	1.9(1)	-	83.3(50)	11.7(7)	5.0(3)
4	13.3(4)	73.3(22)	13.3(4)	-	3.8(3)	74.7(59)	20.3(16)	1.3(1)
5	13.0(3)	78.3(18)	8.7(2)	-	5.9(2)	82.4(28)	11.8(4)	-
6	6.5(2)	83.9(26)	6.5(2)	3.2(1)	4.0(1)	84.0(21)	12.0(3)	-
7	16.7(2)	50.0(6)	25.0(3)	8.3(1)	4.0(1)	68.0(17)	20.0(5)	8.0(2)
8	4.8(1)	57.1(12)	33.3(7)	4.8(1)	-	81.8(9)	9.1(1)	9.1(1)
9	4.8(1)	71.4(15)	19.0(4)	4.8(1)	-	96.6(28)	3.4(1)	-
10	6.3(1)	56.3(9)	37.5(6)	-	3.8(1)	80.8(21)	11.5(3)	3.8(1)
11	-	-	-	-	-	81.3(13)	18.7(3)	-
14	-	-	-	-	-	87.5(7)	12.5(1)	-
17	6.7(2)	73.3(22)	20.0(6)	-	-	-	-	-
19	-	-	-	-	-	83.3(10)	16.7(2)	-
21	-	-	-	-	-	93.8(15)	-	6.2(1)
31	-	-	-	-	-	88.7(47)	11.3(6)	-

(continued next page)

Table 19.--continued

Date	1947				1948			
	II	III	IV	V+	II	III	IV	V
Nov. 17	-	-	-	-	-	-	50.0(1)	50.0(1)
18	-	100.0(3)	-	-	-	-	-	-
19	50.0(1)	50.0(1)	-	-	-	-	-	-
22	-	-	-	-	-	33.3(2)	66.7(4)	-
23	-	94.1(16)	5.9(1)	-	-	-	-	-
24	-	100.0(12)	-	-	-	11.8(2)	82.4(14)	5.9(1)
25	-	-	-	-	-	28.0(7)	68.0(17)	4.0(1)
26	-	-	-	-	-	-	100.0(15)	-
27	-	84.6(11)	-	15.4(2)	-	12.5(2)	75.0(12)	12.5(2)
28	3.6(1)	82.1(23)	10.7(3)	3.6(1)	-	30.0(3)	60.0(6)	10.0(1)
29	-	91.7(22)	4.2(1)	4.2(1)	-	-	-	-
30	11.8(4)	79.4(27)	8.8(3)	-	-	-	-	-
Dec. 1	-	90.0(9)	10.0(1)	-	-	-	-	-
2	2.7(2)	87.7(64)	6.8(5)	2.7(2)	-	20.0(2)	80.0(8)	-
3	-	75.0(27)	25.0(9)	-	-	-	100.0(1)	-
4	-	97.2(35)	-	2.8(1)	-	28.6(2)	57.1(4)	14.3(1)
5	4.5(1)	77.3(17)	13.6(3)	4.5(1)	-	-	-	-
6	8.6(3)	82.9(29)	8.6(3)	-	-	25.0(1)	75.0(3)	-
7	-	82.4(28)	14.7(5)	2.9(1)	-	-	-	-
8	-	100.0(16)	-	-	-	-	-	-
9	2.2(1)	91.1(41)	6.7(3)	-	-	-	-	-
10	3.6(1)	85.7(24)	10.7(3)	-	-	-	-	-
11	-	100.0(9)	-	-	-	-	-	-
22	-	-	-	-	-	100.0(2)	-	-
23	-	-	-	-	-	66.7(2)	33.3(1)	-
28	-	-	-	-	11.1(1)	77.8(7)	-	11.1(1)

(continued next page)

Table 19.--concluded

Date		1949				1950			
		II	III	IV	V+	II	III	IV	V+
Nov.	19	-	-	100.0(1)	-	-	-	-	-
	20	-	-	100.0(3)	-	-	-	25.0(2)	75.0(6)
	23	-	50.0(1)	50.0(1)	-	-	-	33.3(1)	66.7(2)
	27	-	25.0(2)	75.0(6)	-	-	-	-	-
	28	-	6.3(3)	91.7(44)	2.1(1)	-	-	-	-
	29	-	7.4(2)	88.9(24)	3.7(1)	-	-	-	-
	30	-	6.7(1)	86.7(13)	6.7(1)	-	-	-	100.0(1)
Dec.	2	-	-	100.0(19)	-	-	-	37.5(3)	62.5(5)
	3	-	-	50.0(1)	50.0(1)	25.0(1)	-	-	75.0(3)
	4	-	-	100.0(2)	-	-	-	-	-
	7	-	8.3(1)	83.3(10)	8.3(1)	-	-	-	-
	8	-	-	60.0(3)	40.0(2)	-	-	-	-
	9	-	20.0(1)	40.0(2)	40.0(2)	-	-	25.0(2)	75.0(6)
	10	-	-	80.0(4)	20.0(1)	-	-	-	-

SEX COMPOSITION

Changes in sex composition with age

There is considerable variation in the changes in sex composition with age for different cisco populations, some showing an increase in percentage of females, some a decrease, and some no significant change with age (Smith, 1956). The changes in sex ratios with age for different years for the Birch Lake cisco are shown in Table 20. The totals for each age group are given in two separate periods, 1939-1950 and 1952-1965, since the latter shows a much better sampling of the younger age groups. The data indicate no definite trend, although the high percentage of 2-year-old males (age-group I) after 1952 shows that under periods of low population density and rapid growth the males mature at a younger age. This fact is emphasized by Table 21 which gives the average age of the sexes taken during the various spawning seasons. Under high population densities and population decline (1943-1950) the average ages of males and females are very similar, the greatest variation being 0.2 year in 1947 and 1950. However, following the resumption of reproduction and a partial recovery of the population, the males definitely are sexually mature at a younger age. For 9 straight years (1954-1962) the average age of the females is greater, very significantly so for the 6 years of 1955, 1956, 1958, 1959, 1960,

Table 20.--Changes in sex composition of ciscoes with age, 1939-1965

[Number of fish in parentheses; males at left, females at right]

Year	Percent females in age group								
	I	II	III	IV	V	VI	VII	X	Total
1939[a]	100.0 (0:1)	16.7 (5:1)	33.3 (2:1)	-	-	-	-	-	30.0 (7:3)
1943	100.0 (0:1)	25.0 (3:1)	22.4 (114:33)	15.2 (28:5)	16.7 (5:1)	100.0 (0:1)	-	100.0 (0:1)	22.3 (150:43)
1944	-	60.6 (13:20)	40.1 (109:76)	52.5 (28:31)	33.3 (2:1)	50.0 (1:1)	100.0 (0:1)	-	45.9 (153:130)
1945	-	85.4 (6:35)	83.2 (86:427)	90.4 (11:103)	66.7 (3:6)	25.0 (3:1)	-	-	84.0 (109:572)
1946	-	70.0 (3:7)	94.6 (21:369)	93.5 (4:58)	71.4 (2:5)	0.0 (1:0)	-	-	93.4 (31:439)
1947	-	92.9 (1:13)	94.4 (23:391)	90.2 (4:37)	50.0 (3:3)	100.0 (0:2)	100.0 (0:1)	-	93.5 (31:447)
1948	-	100.0 (0:1)	96.8 (1:30)	97.1 (2:68)	100.0 (0:7)	100.0 (0:1)	-	-	97.3 (3:107)
1949	-	-	100.0 (0:11)	98.5 (2:132)	100.0 (0:9)	-	-	-	98.7 (2:152)
1950	-	100.0 (0:1)	-	62.5 (3:5)	87.5 (3:21)	-	-	-	81.8 (6:27)
Totals 1939-1950	100.0 (0:2)	71.8 (31:79)	79.0 (356:1338)	84.3 (82:439)	74.6 (18:53)	54.5 (5:6)	100.0 (0:2)	100.0 (0:1)	

(continued next page)

Table 20.--concluded

Year	I	II	III	IV	V	VI	VII	X	Total
1952	-	-	-	100.0 (0:1)	-	100.0 (0:1)	100.0 (0:1)	-	100.0 (0:3)
1953	-	-	75.0 (1:3)	81.8 (2:9)	72.7 (3:8)	-	-	-	76.9 (6:20)
1954	-	0.0 (1:0)	-	50.0 (7:7)	50.0 (1:1)	66.7 (1:2)	-	-	50.0 (10:10)
1955	4.0 (24:1)	0.0 (1:0)	-	37.5 (5:3)	80.0 (8:2)	-	-	-	27.3 (32:12)
1956	54.5 (10:12)	-	-	100.0 (0:2)	100.0 (0:4)	-	-	-	64.3 (10:18)
1957	-	33.3 (24:12)	100.0 (0:1)	100.0 (0:1)	-	50.0 (1:1)	-	-	37.5 (25:15)
1958	0.0 (4:0)	0.0 (1:0)	69.6 (23:10)	100.0 (0:2)	100.0 (0:1)	0.0 (1:0)	-	-	61.9 (16:26)
1959	46.2 (7:6)	-	72.2 (5:13)	-	-	-	-	-	61.3 (12:19)
1960	4.3 (22:1)	-	100.0 (0:1)	-	100.0 (0:1)	-	-	-	12.0 (22:3)
1961	-	66.7 (9:18)	0.0 (1:0)	100.0 (0:2)	-	-	-	-	66.7 (10:20)
1962	9.8 (37:4)	80.0 (4:16)	-	100.0 (0:2)	-	-	-	-	34.9 (41:22)
1965[a]	83.3 (1:5)	68.8 (5:11)	-	-	-	-	-	-	72.7 (6:16)
Totals 1952-1965	21.6 (105:29)	55.9 (45:57)	48.3 (30:28)	67.4 (14:29)	58.6 (12:17)	57.1 (3:4)	100.0 (0:1)		

[a] Non-spawning population.

Table 21.--Average age of males and females, 1943-1962[a]

Year	Males		Females	
	Average age	Number of fish	Average age	Number of fish
1943	4.23	150	4.09	43
1944	4.14	153	4.15	130
1945	4.18	109	4.15	572
1946	4.26	31	4.14	439
1947	4.29	31	4.09	447
1948	4.67	3	4.79	107
1949	5.00	2	4.99	152
1950	5.50	6	5.70	27
1953	5.33	6	5.25	20
1954	5.10	10	5.50	10
1955	2.75	32	5.42	12
1956	2.00	10	3.22	18
1957	3.16	25	3.47	15
1958	3.63	16	4.15	26
1959	2.83	12	3.37	19
1960	2.00	22	4.67	3
1961	3.10	10	3.20	20
1962	2.10	41	3.00	22

[a] Total age is one year greater than the age group.

and 1962. A study of Table 20 shows a general increase with age in the proportion of females for these years. Dryer and Beil (1964) found, with few exceptions, that the average age of the females exceeds that of the males, although this difference is never greater than 0.5 year. It seems possible, and quite probable, that males mature at a younger age than females under all population conditions, but were not sampled adequately at the younger ages in 1943-1950. Van Oosten (1939) and Van Oosten and Hile (1949) found that the males of the closely related lake whitefish mature 1 year earlier than the females.

Differential mortality and changes in sex composition by years

The most striking variation in sex composition occurs in the total sex ratios for the fish captured during the various years (see Table 20). If a single collection is made during the spawning season, it would be very easy to capture a high proportion of one sex due to sex differences in behavior and to segregation and differential arrival on the spawning grounds. Such a case is illustrated by Cooper (1937) who obtained a sample containing only 29% females. Brown and Moffett (1942), whose sample is based mostly on one collection made late in the season, found twice as many females as males, with the ratio persisting throughout the different age groups. The yearly samples in the present study, however, consist of a number of collections made throughout the spawning season, so inadequate sampling is less of a problem. Nevertheless, it is still important and is illustrated by the years 1952-1965. During this time the sex ratio approaches the expected 1:1 ratio in only one year, 1954. Otherwise there is a marked preponderance of one sex or the other, with the predominant sex fluctuating from year to year. This appears to be due to the differential maturity rates discussed above, with the males predominating when the sample is largely young fish, and the females predominating when mainly older fish are captured. In this light the sex composition obtained for the years 1952-1965 is not unrealistic.

The sex ratios for the years of population decline present a much different problem. It can be seen that the percentage of females increases progressively from 22.3 in 1943 to 98.7 in 1949. The percentage declined to 81.8 in 1950, but only 33 fish were taken in the whole lake that year. Kerle and Washburn (1947)[3] found 85.6% of 940 fish weighed during their study of the cisco harvest in 1945 to be females. Such a tremendous increase in one sex apparently has never been recorded for this species. These sex ratios are not due to differential age at maturity, as was the case after 1952, since the average ages of the sexes are very similar (see Table 21), and there is no significant increase or decrease of either sex with age (see Table 20).

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[3] Kerle, Arthur, and George Washburn. 1947. The cisco harvest from Birch Lake, Cass County, Michigan, in 1945. Michigan Department of Conservation, Institute for Fisheries Research, Rept. No. 1122, 9 p. [Typewritten]

Smith (1956) and Van Oosten (1929) found a progressive decrease in the abundance of females with increasing age, and attributed this to a selective destruction of females in younger age groups, while Dryer and Bell (1964) found the percentage of females increases with age. Since the percentages of females do not increase significantly with age in the present study, it appears there is no differential sex mortality which could account for the lack of males. To test this further Table 22 was compiled and shows the percentage of females in each year class at each successive age of capture. The sex composition for the year classes 1942 through 1948 gives no indication of greater mortality of males, since the sex ratios remain reasonably constant throughout the history of the year class. However, the 1940 and 1941 year classes do show a significant increase in the abundance of females that appears to be due to a heavy mortality of males after their fourth year of life (age III). Since this is the age at which fishing mortality was by far the heaviest, this might be expected to be the cause of the decline in males, if, by chance, a very large proportion of the III age group captured consisted of males. The big change in sex ratio in the 1940 year class occurs between the III age group captured in 1943 and the IV age group captured in 1944. Since the 1943 collection is based on experimental netting and only 2,108 ciscoes of all ages were removed from the lake, this could not have depleted the males in view of the large population then present. The significant increase in the 1941 year class occurs between the III age group taken in 1944 and the IV age group taken in 1945. A total of 18,738 fish were

Table 22.--Sex composition of year classes of ciscoes at successive ages

Age	Year class and percentage of females									
	1938	1939	1940	1941	1942	1943	1944	1945	1946	1948
I	-	-	-	-	100.0	-	-	-	-	-
II	-	-	-	25.0	60.6	85.4	70.0	92.9	100.0	100.0
III	-	-	22.4	40.1	83.2	94.6	94.4	96.8	100.0	-
IV	-	15.2	52.5	90.4	93.5	90.2	97.1	98.5	62.5	100.0
V	16.7	33.3	66.7	71.4	50.0	100.0	100.0	87.5	-	72.7
VI	50.0	25.0	0.0	100.0	100.0	-	-	-	100.0	66.7
VII	-	-	100.0	-	-	-	-	100.0	-	-

taken from the lake in 1944, which certainly means there was considerable fishing mortality. However, since the proportion of the sexes taken in the III age group sample in 1944 is nearly 1:1 (40.1% females), this does not appear to account for an increase to 90.4% females the next year. A more reasonable explanation is that the disappearance of males is due to some environmental factor which is reflected in the abnormal sex ratios throughout the entire year class beginning with 1942, a factor which depressed the males only in the latter stages of the 1940 and 1941 year classes.

Possible determinants of observed sex ratio

Since the sexes arrive on the spawning ground at somewhat different times, it might be argued that the abnormal sex ratios are not indicative of the entire population and are due to sampling the population when the females are more numerous late in the season. It is also possible that there was a shifting in the time and intensity of the spawning runs which, since the population was sampled during the same period every year, might contribute to a shift in sex composition in the catch. Many authors (Smith, 1956; Stone, 1938; Brown and Moffett, 1942; Dryer and Beil, 1964; Washburn, 1944[4]) have observed a critical temperature of 3°-4° C at which ciscoes begin to spawn, so fluctuations in the climate and weather could alter the spawning run.

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[4] See footnote 2, p. 7.

Table 23 is a comparison of the intensities of the spawning runs of 1944-1950. It indicates a very striking similarity in the runs in 5 out of the 7 years. In every year except 1946 and 1948 the peak of the run occurs on either November 30, December 1, or December 2. The general trend of these runs consists of very low catches early in the season, a slow increase to a peak during the first week of December, and then a gradual decline until netting stops, at which point the catch is generally better than that at the beginning of the season. The 1948 run shows no definite peak period, with catch remaining fairly constant throughout the netting period. The low catches at both the start and finish of the season indicate that the run occurred largely during the netting season and was well sampled. The 1946 run was unusually high during the latter part of the season, indicating that perhaps the tail end of the run was not well sampled. However, since males are more numerous early in the season and this part is better sampled, the catch would be biased toward a larger number of males. Actually this appears to be the general rule, rather than the exception. The very low values early in November mean that netting starts well before the main spawning run is under way, and the higher values late in December indicate the run is considerably greater at that time. Because part of the period of female predominance occurs after the season and is sampled less than that of male predominance, the tendency is to select for males, if anything. Since this is the sex which is so scarce, it is concluded that the time of sampling is not responsible for the high number of females.

Table 23.--Daily comparison of catch of ciscoes per hour per net 1944-1950

Date		Year and catch per hour						
		1944	1945	1946	1947	1948	1949	1950
Nov.	15	-	-	-	-	0.07	0.02	0.03
	16	-	-	-	-	0.36	0.00	0.00
	17	-	-	-	-	0.02	0.07	0.00
	18	-	-	-	-	0.00	0.00	0.00
	19	-	-	-	-	0.55	0.00	0.10
	20	-	-	-	-	0.33	0.03	0.00
	21	-	-	-	-	0.72	0.00	0.00
	22	-	-	-	-	0.37	0.00	0.00
	23	-	-	0.17	0.13	0.23	0.16	0.00
	24	-	-	0.88	0.40	0.50	0.07	0.00
	25	8.41	2.68	0.35	0.14	0.35	0.40	0.00
	26	6.72	2.46	0.36	0.37	0.27	0.36	0.00
	27	9.25	4.75	0.57	0.52	0.30	0.35	0.00
	28	7.45	4.54	0.78	0.70	0.20	0.18	0.00
	29	7.28	3.68	0.65	0.71	0.28	0.62	0.00
	30	10.97	5.14	1.17	0.77	0.50	1.87	0.17
Dec.	1	9.31	3.34	0.64	2.28	0.23	0.00	0.00
	2	8.41	4.03	1.58	1.42	0.11	0.80	0.74
	3	6.00	3.93	1.37	0.80	0.18	0.28	0.20
	4	6.64	2.41	1.44	1.70	0.16	0.10	0.33
	5	4.48	2.62	1.64	1.17	0.09	0.10	0.00
	6	3.75	1.75	1.37	0.82	0.15	0.16	0.25
	7	2.90	1.56	1.09	1.40	0.10	0.11	0.00
	8	3.39	2.44	1.67	0.53	0.05	0.30	0.00
	9	2.70	1.08	1.78	0.90	0.05	0.13	0.45
	10	3.49	1.26	1.32	0.60	0.04	0.12	0.13

A further indication of this is that the sex ratio returned to a somewhat normal condition when reproduction resumed and the population increased following its crash.

There was no change in sampling methods between the two distinct periods of male scarcity and abundance. There is always the possibility that the fishermen may have wanted to select one sex, because of better smoking qualities, for example. However, it is not reasonable that the large number of fishermen trying to catch the few ciscoes during the lean years of 1946-1950 would pass up the males. Smith (1956) lists gear selectivity in relation to differential morphology and activity as a possible factor in sex composition. Since males of other species of fish and other types of animals are traditionally the more active sex during breeding periods, it is believed that, if any, male ciscoes move about more and thus are more susceptible to gill netting. Hile and Deason (1947) found males of a closely related species, the kiyi, to be very active during the spawning season. Since there is no significant difference in the growth in length of the sexes of ciscoes in Birch Lake, the only possibility is that the gill nets could select females because of sex differences in weight, shape, and condition at spawning under a period of rapid growth and low population levels which made them more susceptible to gill netting. This does not seem probable, however, because similar rapid growth continued after 1950, and large numbers of males were taken during this period.

This variability in sex ratio cannot be readily explained, although several other possibilities may be mentioned. One is that there was some change in the behavior of the males under low population densities and rapid growth which eliminated them largely from the spawning grounds during the usual spawning season. Smith (1956) found larger ciscoes to spawn earlier than the smaller ones, although this finding was not verified by the present study. It is possible that the extremely rapid growth of males under low population levels may have hastened or retarded sexual maturity to such a degree that they did not spawn normally.

Applegate and Thomas (1965) have studied a closely related problem in the sea lamprey. This is the age at which ammocoete larvae transform into adults and move out of the streams and into the Great Lakes. It is known that there are pronounced changes in sex composition of spawning runs associated with changes in the abundance of upstream spawning migrants in successive years. Applegate (unpublished data cited in Applegate and Thomas, 1965) has demonstrated that the total abundance of spawners and the ratio of males to females was positively correlated in Ocqueoc River, Michigan, spawning runs, that is, the greater the number of mature upstream migrants, the larger was the proportion of males. (This finding is paralleled by the present study in which males are most abundant when the population is high.) A nearly equal sex ratio of recently transformed sea lampreys moving downstream is considered normal. Yet the sex ratio of 1960-61 downstream migrants was 324 males:100 females, an extremely high and atypical proportion of males. This was attributed to two factors. One was the effective prevention of recruitment into the larval populations in the stream for approximately 6 years immediately prior to the 1960-61 downstream run. This was done with barriers which blocked upstream movement of spawners, and resulted in low larval populations. The second factor is that the females apparently transform at an earlier age than do the males. There was no recruitment in 1955-61. In the 5 years between the 1956-57 run and the 1960-61 run the ratio of males to females increased four times. Applegate and Thomas conclude that such a pronounced shift in sex composition can mean only that the females transform and leave the stream at an earlier age under low larval population densities in the stream. This fact can then be correlated with the relative abundance of females when the adult spawning population is low and the relative abundance of males in high spawning populations, when it is considered that, one growing season later, these downstream migrants form the basis for the next spawning run.

Perhaps a slight seasonal variation in maturity or behavior associated with low populations may have occurred in male ciscoes in Birch Lake. Since the population was under obvious stress during this period it seems logical that any change would be such as to increase the survival chances of the species. A higher percentage of females on the spawning grounds may be construed as a step in this direction, since the cisco is a pelagic spawner, and a single male may spawn with several females. However because the sexes do tend to segregate on the spawning grounds and because so very few males were present, it appears that reproduction may be reduced rather than increased under such sex ratios.

Possible determinants of actual sex ratio

If differential mortality, changes in behavior and time of maturity, sampling errors, segregation on the spawning ground, gear selectivity, and variations in the spawning runs are discounted, then it must be assumed that the observed sex ratios are the true sex ratios of the population. Such an assumption points to the related concepts of intersexuality, parthenogenesis, sex reversal, hermaphroditism, sex differentiation and determination, and genetic abnormalities for an answer. Much of the material on these subjects has been treated by Atz (1964) and no attempt will be made to explain them. These phenomena will be mentioned here only as they might apply to the immediate problem and anyone wishing a more thorough explanation should consult Atz (1964).

Melander and Monten (1950) report a case of probable parthenogenesis in Coregonus lavaretus in which 15% of a batch of unfertilized eggs developed into females. Turdakov and Turdakov (1959) found that ova of about 40% of female Leuciscus bergi developed parthenogenetically. The percentage of eggs which developed parthenogenetically varied from 1% to 90% in different females. In this instance, however, external impregnation of the ova by spermatozoids was necessary for development. Nevertheless it is shown that parthenogenesis has occurred in the families Coregonidae and Cyprinidae. It is known that some type of mortality greatly reduced the males in the 1940 and 1941 year classes of the cisco. If a large number of females had no males with which to mate, conditions for parthenogenesis could exist if the females spawned anyway. Such parthenogenesis, if it did occur, would then contribute to the larger percentage of females, since these eggs would develop into females. The possibility that a limited amount of parthenogenetic development may occur naturally, but is not significant under normal reproductive conditions when both sexes are prominent and the percentage of fertilized eggs is high, may also be considered.

Although these phenomena are known to occur in many fish, the literature does not indicate that hermaphroditism or sex reversal may be operative in coregonids. Also no literature was found which supported the possibility of the sex ratio at fertilization being altered by unusual conditions, either environmental or genetic. One more logical explanation involves the period of sex differentiation when the fish is very young. Here there is the possibility that strong environmental conditions may influence sexual development in one direction. Atz (1964) writes concerning the effect of the environment on sex ratios (p. 193): "Scientific investigation of environmental influences on sex determination and differentiation in fishes has yielded a number of provocative and little understood observations. That the environment can exert, under some circumstances, a significant effect on the sex ratio is well established, but how this is accomplished is unknown, and even the conditions under which it occurs are ill-defined. The problem of ruling out differential mortality must always be faced and is especially acute in forms, like the oviparous fishes, that exhibit high fecundity with a significant amount of mortality under the best of conditions." Dr. Atz points out that investigators of this problem have found that crowding and starvation result in higher proportions of males and then continues (p. 194): "It is interesting to note that as far as known among teleosts, adverse environmental conditions appear to favor the differentiation of males, and yet the males are the less viable sex, as measured by longevity and resistance to adverse environmental agents. Is this adaptive?" The fact that male ciscoes were numerous when the population was high and growth slow, and then declined in abundance when the population decreased and growth increased, seems to be evidence in support of the above statements. Hile (1936) concluded that (p. 292) "the correlation between growth rate and sex ratio may be considered to result from the dependence of these two characteristics on the same environmental factors."

It is most important here to differentiate between the individual and the species. While environmental conditions, as measured by growth, seemed poor for the individual, they were apparently better for the species as a whole, as indicated by the high population levels and successful reproduction. When the conditions, as measured by growth, seemed good for the individual, they apparently were much worse for the species since the population was undergoing a marked reduction in numbers and in amount of reproduction, leading almost to extinction. In Birch Lake environmental conditions as they affect the individual cisco are the important ones in influencing the determination and differentiation of sex, if such a phenomenon does occur. Perhaps growth is not the best criterion to use here since after 1950 the sex ratio returned to normal under continuing rapid growth. The success of reproduction may be a better indicator of these environmental conditions that may alter the sex ratio, i.e., conditions are better for the individual when reproduction of the species as a whole is poor. The entire problem is one of cause and effect.

REASONS FOR POPULATION FLUCTUATIONS

A final discussion of the possible factors responsible for the population fluctuations of the cisco in Birch Lake serves to emphasize the complexity of the relationship between an organism and its environment. Because of the many interactions between the various ecological conditions and the complexity of their effects on the cisco, it is not possible to determine if any one factor is responsible for the changes, although several factors may be largely eliminated.

Overfishing

One influence that must be considered is overfishing. Washburn (1945)[5] and Kerle and Washburn (1947) (see footnote 3), using computed average weights, calculated that ciscoes were removed during the netting season at a rate of 32.9 pounds per acre in 1944 (10,540 pounds total) and at a rate of 23.3 pounds per acre in 1945 (7,168 pounds total). The 1944 value seems especially high in view of the great depth and relatively low productivity of the lake. Carlander (1955) gives the average standing crop of fish in "trout" lakes as less than 50 pounds per acre. Since the ciscoes are all caught within such a short period these values are comparable and could possibly indicate overharvesting of the stock, considering that the cisco is only one of many species of

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5 Washburn, George N. 1945. The cisco harvest from Birch Lake, Cass County, in 1944. Michigan Department of Conservation, Institute for Fisheries Research, Rept. No. 1020, 12 p. [Typewritten]

fish in the lake, and especially since the three youngest and most numerous age groups of ciscoes are hardly harvested at all. However, the cisco is a plankton feeder and therefore is in a relatively low trophic level, where productivity is greater than for the higher predator levels in which most other fresh-water sport and commercial fish species are found.

A review of the age structure of the population during its decline (see Table 8) indicates that overexploitation was probably not the main contributor to the fluctuations. Van Oosten (1929) lists three symptoms of heavy commercial fishing, namely (1) the paucity of old individuals, (2) the shifting in the age composition of the samples, and (3) the one-year dominance of a year class. However, Scott (1951) felt that in Lake Erie, where the fishery was quite intense, the dominance of the cisco fishery over a number of years by one year class was the rule rather than the exception. Symptoms (1) and (3) are certainly present in the present data for 1943-50 and indicate heavy fishing, although they are undoubtedly due also in part to gear selectivity. Symptom (2), which involves the increase in the percentage of young fish in the catch at the expense of the older, is definitely not true in the present study, since the population actually ages 1.32 years from 1946 to 1950. This indicates that a lack of reproduction was more responsible for the decline in the population. Carlander (1945) found a marked change in the size and age composition of the cisco population resulting from changes in fishing intensity. He found intense fishing resulted in the establishment of populations of young small fish. The ciscoes in Birch Lake became big and old when the population declined. Even if fishing mortality was high, Scott (1951) has shown that a large spawning stock is not necessary for a successful year class. The commercial catch of ciscoes in Lake Erie in 1943 was the lowest recorded since 1871. Yet the year class spawned by this stock was one of the largest ever produced. The cisco has such a high fecundity and reproductive potential that the factors influencing hatching and survival are much more important (Scott, 1951). Pritchard (1951) feels that factors other than overfishing are responsible for the population fluctuations of the cisco in Lake Ontario.

Trout stocking

There is the possibility that stocking of trout may have contributed to the changes in the cisco population. Table 24 gives the kinds, numbers, and sizes of trout planted in Birch Lake by the Michigan Department of Conservation. The period of heavy rainbow trout stocking, 1940-1953, coincides largely with the period of population decline of the cisco. The cisco population made a considerable comeback after 1953 when trout were stocked only every 3 or 4 years. This may be coincident or it may mean that the trout contributed to the decline. Leonard and Leonard (1947), who studied the food habits of rainbow and lake trout in Birch Lake, concluded that the trout were not significantly predatory on the cisco, did not compete with it for food to any degree, and did not appear to jeopardize the cisco population in any way.

Table 24.--Trout stocked in Birch Lake, 1907-1963

Year	Rainbow trout		Lake trout		Brook trout		Brown trout	
	Number	Size	Number	Size	Number	Size	Number	Size
1907			10,000	fry				
1908			10,000	fry				
1909			10,000	fry				
1910			10,000	fry				
1937			10,000	9 mo				
1938	1,000	yrlgs			1,000	yrlgs		
1940	2,000	yrlgs	790	adults				
1941	4,786	7 1/2 mo						
1942	2,510	8 mo						
1943	4,519	yrlgs						
1944	3,000	14 mo						
	2,763	23 mo						
1945	2,763	14 mo						
	3,026	22 mo						
1946	3,003	13 mo						
	3,000	23 mo						
1947	3,000	yrlgs					5,000	yrlgs
	3,000	yrlgs						
1948	3,000	7.5"					5,000	4"
	3,000	9.0"						
1949	3,000	8.0"					5,000	4"
	3,000	10.0"						
1950	3,000	7.0"					5,000	4"
	3,000	10.0"						
1951	3,000	7.0"						
	3,000	8.0"						
1952	3,600	4.5"						
1953	3,000	8.5"						
1956	6,000	legal						
1959	6,000	legal						
1963	2,400	legal						
Total	83,370		50,790		1,000		20,000	

Parasites, predators, and competitors

Numerous species of warmwater fish are present in Birch Lake, but these would not seem to compete with or feed upon the cisco, which remains in deeper water throughout most of the year. Gar control was carried out in the lake for a number of years and this predatory fish may have been present in considerable numbers. However, it is known to remain near the surface in the warmer upper stratum of water.

Yellow perch and bullheads have been found to be important predators of cisco eggs, as are the ciscoes themselves (Stone, 1938; Pritchard, 1931). Personal communication with workers on Birch Lake has indicated that the perch is an especially important egg predator. Table 25 gives the catch per hour per net of perch and cisco taken during the various years, and also the catch of non-cisco fish per hour per net and the percentage of the total fish that were non-cisco. The increase in the proportion of fish caught that were not ciscoes is due mainly, of course, to the reduction in the cisco population. There is some increase in the catch per hour of perch and other warmwater fish, but the increase does not seem to be significant enough to increase competition and predation to where it could cause the striking decrease in ciscoes. It is very important to realize that the fish sampled are mostly predatory game fish, and that there is no indication of the numbers of minnows in the lake. Since many of these fish occupy the

Table 25.--Catch of ciscoes and other fish, 1939-1950

Year	Percentage non-cisco	Perch per hour	Non-cisco per hour	Cisco per hour
1939	0.65	.014[a]	.03[a]	4.5[a]
1943	2.15	.036	.067	3.07
1944	1.62	.06	.10	6.28
1945	3.47	.035	.13	3.15
1946	9.1	.06	.11	1.07
1947	21.7	.17	.22	0.78
1948	32.3	.067	.11	0.24
1949	49.7	.11	.19	0.19
1950	47.9	.13	.16	0.17

[a] Based on 6 hours per set, the lawful set time beginning in 1944.

same trophic level as ciscoes, the possibility of increased competition from small, plankton-feeding fish cannot be ruled out.

In many areas ciscoes are often heavily parasitized, especially by worms of various kinds. Carlander (1945) found it was advisable to reduce the population in order to get greater production of non-parasitized fish. Under maximum population levels the ciscoes contained so many larvae of the tapeworm Triaenophorus robustus that the fish were banned from sale on the market. Pritchard (1931) found that the ciscoes of Lake Ontario were not heavily infested with parasites, while Hile (1936) found the ciscoes in three out of the four lakes studied had a very high (80% or more) positive incidence of parasites. One population was almost free of parasites and showed by far the best growth rate, although both factors are undoubtedly also linked closely to the population size.

Parasitism is not a major source of mortality in the cisco population in Birch Lake. The few specimens examined by the author failed to reveal any parasites, and workers on the lake have consistently said that the species is remarkably parasite-free even under high population densities.

Aging of the lake

It is often said that all lakes are doomed to extinction of "death." They age as surely as an organism ages and pass through periods of youth, middle-age, and old-age, called oligotrophy, eutrophy, and dystrophy by many limnologists. As the lake ages and its limnology changes, so does the community of organisms in the lake change. Frey (1955), in his very interesting study, makes the assumption that the cisco once was present in all the glacial lakes in the watersheds where it has occurred, and that its present day absence from a lake means the lake has aged and environmental conditions unsuitable to the survival of the cisco have developed. It is possible that the changes in the cisco population in Birch Lake reflect changes in the physical, chemical, and biological make-up of the lake itself.

Despite its southerly geographic location, Birch Lake still can broadly be considered to be oligotrophic, or young, because of its depth and large volume of cold water. As such it appears to remain as excellent habitat for the cisco. Frey (1955) established a minimum tolerance limit of 3 ppm of dissolved oxygen, and a maximum tolerance limit of 20° C temperature for the species. Limnological data taken in 1937 and shown in Table 26 indicate the lake to be very suitable for ciscoes, with an abundance of oxygen on the bottom. No limnological records were kept after this date. In the summer of 1942 or 1943 Mr. C. Troy Yoder, in checking for the lower limit where rainbow trout might be located, found that the oxygen was completely gone on the bottom, but that it was 4 ppm or over down to 75 feet (personal communication). Data taken on August 10, 1965, is also shown in Table 26, and indicate further depletion in the dissolved oxygen content, since it is not suitable for ciscoes much below 50 feet.

Table 26.--Comparison of limnology of Birch Lake, 1937 and 1965

July 8, 1937			August 10, 1965		
Depth (feet)	Temperature (°F)	Oxygen (ppm)	Depth (feet)	Temperature (°F)	Oxygen (ppm)
0	80.2	8.3	0	73.5	8.4
6	78.6		2	73.5	
9	76.3		4	73.5	
12	75.2		6	73.5	
15	73.0		8	73.5	
18	72.3		10	73.5	
21	70.2		12	73.0	
24	64.8		14	73.0	
27	57.2	8.2	16	73.0	
30	53.8		18	72.5	
36	50.5		20	72.0	8.2
39	50.0		22	70.5	
42	-		24	67.0	10.9
45	50.0	8.3	26	60.5	
60	46.8		28	56.0	
75	46.0		30	52.0	
95	44.6	4.6	32	49.5	12.8
96	-		34	48.0	
			36	46.0	
			38	45.0	
			40	44.5	
			42	44.0	
			44	43.5	
			46	43.5	
			48	43.0	
			50	43.0	3.5
			60	42.5	2.3
			70	42.0	1.4
			80	42.0	0.5
			90	42.0	0.0
			95	42.5	0.0

Although the vertical oxygen distribution tends to indicate eutrophication and an increase in productivity, these comparisons do not take into consideration the date, climate, weather, and other factors. It is possible that this much variation could occur in one summer if careful records are kept. Hile (1936) found the poorest coefficient of condition of the cisco to be in the most eutrophic environment, and the best condition in the most oligotrophic environment. Although adverse limnological conditions cannot be ruled out as a cause of the population crash in the 1950's, it is felt that at present the lake is not much changed as cisco habitat from the period of high population level. This conclusion is based largely on the above findings of Hile and the fact that ciscoes presently grow big and fat in Birch Lake.

A reduction in total biomass of ciscoes has not necessarily occurred when comparing the high population densities and the present lower ones, since the average size of the fish is currently much greater and growth much better. It appears that although eutrophication may have lowered the amount of habitat at certain times of the year, the lake has maintained or increased plankton food levels so that the remaining fish can grow better and maintain the level of overall cisco production.

Cycles

The final possible explanation is one expressed by many fishermen and workers who are familiar with Birch Lake and the other nearby cisco lakes. This is that there are more or less predictable cycles which occur in the cisco populations. Such periodic fluctuations would be similar to the well known population cycles of Arctic birds and mammals, and such fish as sockeye, pink, and Atlantic salmon (Scott, 1951). That violent non-periodic fluctuations occur in this species in both inland waters and the Great Lakes was established very early in this paper. However, there is no indication in the literature that population cycles do exist in this fish. As Errington (1954) points out, a tremendous amount of very convincing data would have to be accumulated before the presence of a "cycle" could be proven.

It is known that the individual cisco lakes in the Cass County cluster to which Birch Lake belongs do not all show population peaks or declines at the same time. During the late 1940's when the population was so low in Birch Lake, Shavehead Lake, which is only about 2 miles away, is said to have produced an almost unbelievable number of ciscoes, 500 ciscoes per net per night being an "average" catch (personal communication with Mr. Gerald Breece). This indicates that climate is not the determining factor in such fluctuations, but that they are dependent on the ecological conditions in each individual lake. Hile (1936) also found that the length of the cisco's growing season and the abundance of a year class depend on the local conditions and not on general climatic conditions that affect all lakes the same.

SUMMARY

1. The shallowwater cisco is a short-lived, fall-spawning member of the whitefish family found in the Great Lakes and deeper, colder inland lakes. It is very plastic morphologically.

2. This species is known to show violent non-periodic fluctuations in population numbers.

3. Birch Lake is a lake of 295 acres with a depth of 95 feet and is characterized by an abrupt slope at the drop-off, a large volume of hypolimnetic water, and a sparse growth of aquatic plants.

4. A gill-net sport fishery for ciscoes exists during the fall spawning season. The catch records show a marked decline in the cisco population in the years 1939-1950.

5. A total of 2,839 scale samples were aged to study age and growth of the cisco, all but 71 of which were taken during the spawning season. The fish were captured in gill nets.

6. Not all the scale samples were taken from the same area of the body.

7. Plastic impressions were made of the scales and the scales were aged with the aid of a microprojection machine. The formation of accessory annuli was found to vary with the year, the age of the fish during that year, and the growth rate of the fish.

8. There was no significant difference between the length at capture of male and female ciscoes.

9. Gear selectivity results in very narrow length ranges and small differences in size among the age groups. Also the age composition of ciscoes taken from gill nets is not representative of the population. Length is not a good indication of age.

10. The length of the individual fish increased as the number of fish in the population decreased.

11. A study of year class strength showed that the decline in population numbers was due to a lack of reproduction in the latter 1940's. In 1943-47 mostly age-group-III fish were taken. Then the population began to age in 1948 with the onset of poor reproduction and remained so until 1954. The year 1955 marked the return of younger fish to the spawning population. The fish were maturing so much younger that the fishery now selected for age-groups I and II, as it had for the III age group previously.

12. The body-scale relationship based on 1, 226 fish gave an unsatisfactory estimate of the size of the fish at scale formation. It was necessary to use the anterior radius measurement and the direct-proportion method of calculation of growth. This method gave consistent calculations for all except the first year of growth. Lee's phenomenon occurs in comparisons among age groups of different year classes and also among age groups of the same year class.

13. With high population density, growth was rapid during the first 2 years of life but decreased markedly thereafter. Under low

density growth was much more rapid during later years of life but was about the same as under high density for the first 2 years. This suggests that growth is largely density independent during the first 2 years but is density dependent thereafter. Overall growth is not greatly limited by maturity but rather by population size, and there is little competition between young and old fish.

14. Females weigh significantly more than males during the spawning season.

15. The length-weight relationship varies by sex, season, progress of spawning, and year of capture. The overall relationship based on 2,567 fish is

$$\text{Log } W = -3.13615 + 3.82606 \text{ Log } L$$

where W is weight in ounces and L is total length in inches. Growth in weight was not calculated because the fish were captured during the spawning season. The length-weight relationship of spawning males fits a log-log equation better than spawning females.

16. Males precede the females to the spawning ground to some degree but this is not always pronounced. Older and larger fish were not found to spawn earlier.

17. There is no definite change in the sex composition with age under high population density and the period of population decline. Under lower stable population levels, males mature at a younger age, so there is an increase in the proportion of females with increasing age.

18. An abnormally large percentage of females appeared in the spawning run during the period of population decline. The percentage of females increased from 22.3 in 1943 to 98.7 in 1949 and then declined to 81.8 in 1950 when only 33 fish were taken. The sex ratio returned to normal when the population recovered.

19. Differential age at maturity and natural and fishing mortalities are not responsible for the lack of males, although males did suffer a high mortality in the 1940 and 1941 year classes.

20. Variations in the spawning run, changes in behavior and time of maturity, sampling errors, segregation on the spawning ground, and gear selectivity are discounted as causes of the unusual sex ratios. Possible explanations of the sex ratio are parthenogenesis and environmental effects on sex differentiation.

21. Overfishing, trout stocking, parasites and predators, climate and changes in the limnology of Birch Lake are apparently not responsible for the population fluctuations of the cisco. Increased competition from small fish and the existence of population cycles cannot be ruled out, although there is also no evidence in support of these factors as causes of the fluctuations.

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